Detecting and Decomposing the Sources of Variation in Habitat Selection of Large Herbivores in Space and Time

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Diplom Biomathematikerin
Claudia Dupke
aus Waren(Müritz)

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Prüfungsausschuss:

PD Dr.	Björn Reineking	(Erstgutachter)
Prof. Dr.	Michael Hauhs	(Zweitgutachter)
Prof. Dr.	Cyrus Samimi	(Vorsitz)
Prof. Dr.	Thomas Koellner	

Summary

Movement of animals is a key element in maintaining ecological processes. In particular, biodiversity is stabilized through movement behaviour of animals as moving animals provide connections between resources, genes and processes of otherwise isolated areas. How and why animals move on small or greater scales is therefore of utmost importance. For more than three decades, researchers aim to understand patterns of animal movements by disentangling the complex cause-effect relationship between the internal state of individuals and external conditions of their environment that leads to the observed movement paths of animals. This study is a methodological contribution to the analysis of animal movements with respect to the site selection of animals.

The process of movement is continuous in space and time, which is usually discretized for the purpose of analysis. Based on the resolution of discretization, movement can be analysed on different scales ranging from a small scale to broader scale processes. The analysis of movement data is scale-dependent and so is its inference. Processes on greater scale are assumed to be more strongly linked to fitness related processes as survival and reproduction than processes on smaller scale. However, as movement patterns of greater spatio-temporal scales results from small-scale individual movement decision a fundamental understanding of movement can only be obtained by a multi-scale approach. A hierarchical approach to understand the process of movement is crucial to disentangle the interaction between animal and its environment.

In this thesis various approaches are applied to analyse the response of animals to environmental factors. For the analysis we used environmental and movement data from the National Park Bavarian Forest, Germany, recorded between 2002 and 2011. GPS-based location data of roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) were analysed on different temporal and spatial scales with conventional methods such as resource selection functions, approaches from other fields as multicategory logit models, as well as novel approaches as step selection functions and individual based models. The aim was to identify and quantify sources of variation in the site selection of animals.

By analysing roe deer movement data, we revealed distinct *temporal* variation in habitat selection of roe deer on different temporal scales, whereby daily and seasonal scales interacted. The fine-scale temporal variation of habitat selection by roe deer followed a nycthemeral cycle change mostly associated with daily variation of human disturbance. In contrast, the larger-scale seasonal variation in habitat selection followed plant growth, and hence mostly in response to food resource. Beside temporal variation, we tested for *spatial* variation in habitat selection, namely the effect of the availability of a habitat on the selection, known as functional response. We found distinct patterns of functional response for different habitat types. We further revealed that the type of functional response varied with time of day and time of year. We referred the shape of the functional response to the trade-off in the choice between food and cover.

Furthermore we quantified the degree of variation in habitat selection that is due to differences between and within *individuals* which relates to the plasticity in the behavioural response towards changing conditions of a species. A framework is presented for partitioning variation in habitat selection into between- and within-individual variance components. Our analysis on red deer showed that consistency in site selection behaviour and the degree of concordance among individuals varied over the time of day. This study provides an approach for assessing the ability of a species to adapt to changing environmental conditions. These information are of particular significance for conservation management given the ongoing habitat loss and alternations.

Finally, we present a model technique that integrates the movement process in the analysis of habitat selection, called *individual-based movement* model. This approach does not only analyse habitat selection in a descriptive way, but also allows the researcher to simulate movement of animals given a changing environment. This is in particular relevant for evaluating management scenarios in advance. Methodological approaches presented in this theses are supposed to contribute to an improved understanding about the ecology of animals, in particular about the movement behaviour. A profound knowledge about the ecology of animals should guide conservation planning. Given the ongoing loss of biodiversity and the associated high level of species extinction, scientific studies can become an important cornerstone in nature conservation.

Zusammenfassung

Das Bewegungsverhalten von Tieren ist zentral für den Erhalt ökologischer Prozesse. Durch ihr Streif- und Wanderungsverhalten stabilisieren Tiere insbesondere die Biodiversität, da sie Bindeglied zwischen räumlich ursprünglich getrennten Ressourcen, Genen und Prozessen sind. Wie und warum Tiere sich auf ihre ganz spezielle Art und Weise im großen wie im kleinen Maßstab bewegen, ist daher von großem Interesse für die Wissenschaft. Seit mehr als drei Jahrzehnten, versuchen Forscher Muster von Tierbewegungen zu verstehen. Dabei gilt es, die komplexen Kausalzusammenhänge der individuell-internen Bewegungsauslöser einerseits, der externen Umweltfaktoren andererseits, sowie deren Wechselwirkung zu entschlüsseln, die zu den beobachtbaren Pfaden der Tiere führen. Die vorliegende Arbeit ist ein methodischer Beitrag in der Analyse von Bewegunsgdaten von Tieren im Bezug auf die Ortswahl.

Der Fortbewegungsprozess an sich ist zwar kontinuierlich in Raum und Zeit, für eine Analyse hingegen, wird er diskretisiert. Abhängig von der Auflösung der Daten kann der Fortbewegungsprozess auf unterschiedlichen Skalen analysiert werden. Eine feinskalige Analyse erlaubt allerdings nur einen feinskaligen Einblick in das Bewegungsverhalten, während grobskalige Analysen Auskunft über das Bewegungsverhalten über längere Zeiträume und größere Räume erlauben. Es wird angenommen, dass Prozesse auf großer Skala fitnessbezogene Vorgänge wie Überleben und Fortpflanzung eines Tieres stärker beeinflussen als kleinskalige Prozesse. Da aber Prozesse auf großer Ebene durch Prozesse auf kleiner Ebene beeinflusst werden, ist eine Analyse auf mehreren Ebenen notwendig, um das Bewegungsverhalten von Tieren in Abhängigkeit von Umweltvariablen als Ganzes zu verstehen.

In der vorliegenden Arbeit werden verschiedene Ansätze beleuchtet, die die Reaktion von Tieren auf Umweltfaktoren untersuchen. Dafür wurden Bewegungsdaten aus dem Nationalpark Bayerischer Wald verwendet, die zwischen 2002 und 2011 erhoben wurden. Für die Analyse von GPS-Daten von Reh (*Capreolus capreolus*) und Rothirsch (*Cervus elaphus*) verwendeten wir konventionelle Methoden wie *Resource Selection Functions*, Ansätze anderer Disziplinen wie *Multikategorielle Logit Modelle*, als auch neuere Herangehensweisen wie *Step Selection Functions* und *Individuen-basierte Simulationsmodelle*. Unser Ziel war es, Ursachen für Veränderlichkeiten im Bewegungsverhalten, speziell der Habitatselektion, zu identifizieren.

Eine wichtige Komponente ist *Zeit*. Dafür analysierten wir die Auswahl von verschiedenen Habitaten durch Rehe über mehrere räumliche und zeitliche Skalen. Es stellte sich heraus, dass die tageszeitliche und jahreszeitliche Skalen interagieren, wobei sich auf tageszeitlicher Skala die Störung durch den Menschen als größter erkennbarer Einfluss zeigte, während sich auf der jahreszeitlichen Skala der saisonale Verlauf des Pflanzenwachstums stärker widerspiegelte. Neben der zeitlichen Komponente, untersuchten wir den räumlichen Effekt der Verfügbarkeit eines Habitats auf dessen Auswahl, bekannt auch als *functional response*. Wir zeigen verschiedene Muster von *functional response*, die tages- und jahreszeitenabhängig sind. Die verschiedenen Muster konnten wir auf einen Trade-off in der Wahl zwischen Nahrung und Deckung zurückführen.

Eine weitere Quelle von Variabilität in der Habitatselektion ist *Individualität*. Wir präsentieren erstmalig eine statistische Methode, die die Varianz in der Habitatselektion in Varianz zwischen Individuen einerseits und Varianz innerhalb der Individuen andererseits unterteilt. Wir zeigen, dass das Ortswahlverhalten von Hirschen zu manchen Tageszeiten konsistenter ist als an anderen, sowie dass die untersuchten Tiere sich zu bestimmten Tageszeiten stärker in ihrer Ortswahl unterscheiden als an anderen. Unsere Methode erlaubt es zu quantifizieren, wie variabel Populationen auf schwankende Umwelteinflüsse reagieren und damit wie groß ihre Flexibilität und Anpassungsfähigkeit ist.

Schließlich wurde ein Modell angewendet, das das Bewegungsverhalten der Tiere in die Analyse der Orstwahl einfließen lässt. Dieser Ansatz erlaubt nicht nur eine beschreibende Auswertung der Habitatwahl, sondern ermöglicht zusätzlich eine Bewegungssimulation unter veränderten Rahmenbedingungen. Das ist außerordentlich relevant für Managementmaßnahmen, die im Vornherein evaluiert werden sollen. Grundlegendes Wissen über das Bewegungsverhalten von Tieren ist notwendig, um nachhaltige Maßnahmen in Tier- und Naturschutz sinnvoll zu planen.

Contents

Chapter 1

Introduction

1.1 Motivation of the thesis

Anthropocene is the suggested name of the new human-dominated geological epoch in which we live today (Crutzen, 2002). The term illustrates the fact that mankind's influence on the Earth's environment has reached global significance. The human population has explosively grown in recent decades with a subsequent impact on its environment. About 30-50% of the planet's land surface is utilized by humans (Vitousek et al., 1997). Side effects of the massive exploitation are deforestation (van der Werf et al., 2010), river diversion and dam building (Gregory, 2006), agricultural land conversion and intensification (Matson et al., 1997), emissions of oxides substantially overriding natural emissions (Crutzen, 2002), release of toxic substances into the environment (Koehler and Triebskorn, 2013), urbanization (Turner et al., 2004) and introduction of alien species (Ordonez et al., 2010), to name a few. Outcomes of anthropogenic activities are various. But all have in common to cause land transformation such as habitat destruction which leads to ecosystem simplification and a loss of biodiversity[1] (Tilman et al., 2001).

For example, agricultural intensification under the heading of the *Green Revolution* often leads to monoculture due to the reduction of crop or livestock species. Population abundance and taxonomic diversity of the macrofauna in agricultural systems were shown to be less than half of that in a primary forest (Matson et al., 1997). Biodiversity loss is known to reduce the efficiency in biological cycles like resource capture and biomass production which has consequences for all trophic levels (Cardinale et al., 2012). A ecosystem that is diverse in terms of species coexistence is known to be more stable

[1]The United Nation's Convention on Biological Diversity defines biodiversity as: "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species, and of ecosystems." (United Nations, 1992)

since different life forms can respond more differentially and operate compensatorily through *equalizing* and *stabilizing* effects[2] (Chesson, 2000).

However, biodiversity has been shown to decline continuously over the past four decades indicated by decreasing population sizes of different kinds of indicator species and an accelerated extinction risk of species (Butchart et al., 2010). Researchers already discuss whether the loss of species over the past few centuries and millennia can be considered to be a mass extinction meaning the extinction of more than three-quarters of species in a geologically short interval (Barnosky et al., 2011). The effect of the extinction of one species within an ecological network can be propagated through multiple trophic levels, causing secondary extinctions and extinctions cascades[3] (Colwell et al., 2012).

Efficient contribution for maintaining biodiversity are the preservation of valuable habitats and threatened species (Margules and Pressey, 2000). Besides the discussion about how massive the actual extinction is, there is still a high diversity in wildlife and many species left, that require human effort to be saved. Today, 15.4 % of the earth's terrestrial area and 8.4 % of the marine areas belongs to protected areas[4] (Juffe-Bignoli et al., 2014). Targets of those protected areas are effectiveness, equitability, connectivity and ecological representation of ecosystems[5]. In protected areas biodiversity is aimed to be increased. One goal is to conserve threatened species[6].

But the question is how should endangered species be conserved that face habitat alteration and loss? Conservation management in ecology intervene in ecosystems to maintain or increase biodiversity. Management plans and realizations were earlier based

[2] "(a) equalizing because they tend to minimize average fitness differences between species, or (b) stabilizing because they tend to increase negative intraspecific interactions relative to negative interspecific interactions" (Chesson, 2000)

[3] This effect is known as coextinction, which is the "extinction of a species as a consequence of its dependence on another that has gone extinct or declined below some threshold abundance" (p.184, Colwell et al., 2012)

[4] Definition of the United Nation's Convention on Biological Diversity:""Protected area" means a geographically defined area which is designated or regulated and managed to achieve specific conservation objectives" (United Nations, 1992)

[5] In 2010, a Strategic Plan was adopted by the 192 State Parties to the Convention on Biological Diversity. The plan included the 20 Aichi Biodiversity Targets, which are aimed to be achieved by 2020. Target 11 states: "By 2020, at least 17 per cent of terrestrial and inland water areas and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscape and seascape. "(Juffe-Bignoli et al., 2014)

[6] Target 12 of the 20 Aichi Biodiversity Targets: "By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained." (Juffe-Bignoli et al., 2014)

on experience and intuition (also known as "expert-based", Stalmans et al., 2001; Guisan and Thuiller, 2005). Today, science is becoming an important cornerstone in nature conservation. Science can support in three ways (deduced from Margules and Pressey, 2000):

- Construction of policies based on scientific theory
- Implementation of policies and conventions
- Evaluation of effectiveness of interventions

Scientific studies that guide conservation planning are rarely found in the scientific literature but are more and more commonly used in practice (Guisan et al., 2013). For example, such studies involve the identification of critical habitats (Heinrichs et al., 2010), selection of conserved areas (Ferrier et al., 2002) and managing invasive species (Soberon et al., 2001). Science can support reintroduction programmes of extinct species by spatially explicit dispersal models that helps to specify road-crossing management or the selection of release points (Kramer-Schadt et al., 2004).

One prerequisite for protecting threatened species is to understand their ecology which is associated with fitness. Fitness of a species is related to gene flow and genetic variation (Shafer et al., 2012), metapopulation dynamics (Hawkes, 2009) and local or global persistence of a population (Lindenmayer and Possingham, 1996) which all are linked to biodiversity (Baguette et al., 2013). Hence, fundamental knowledge about the functioning of cause and effect in the alteration of animal behaviour will provide a guide to how biodiversity can be increased in ecosystems. The questions asked by researchers concerning the ecology of animals are (modified from Cagnacci et al., 2010):

- *Why* and *how* do animals move (Nathan et al., 2008)?
- *Why* and *how* do animals use specific resources (Forester et al., 2009)?
- *Why* and *how* do animals avoid being killed (Lima, 1998)?
- *Why* and *how* do animals ensure reproduction (McLoughlin et al., 2006)?

All these questions are related to the spatial behaviour of animals. Ecology is fundamentally spatial, meaning that ecological processes are affected by the landscape configuration, such as the spatial distribution and composition of resources (Cagnacci et al., 2010). The effect of various factors on the ecology of animals vary over the landscape as their presence, intensity or other antagonists effects vary over space. The spatial heterogeneity of influencing factors and the spatial distribution of animals are pointers to the drivers of biodiversity.

In particular, movement of animals is a key element for the conservation of biodiversity (Jeltsch et al., 2013). Moving animals are mobile units that provide connections

between resources, genes and processes of otherwise isolated areas. Connectivity of the landscape is fundamental for the maintenance or structuring of biodiversity (Baguette et al., 2013). Movement can further operate as *stabilizer* or *equalizer* in the mediation of coexistence of communities as mobile individuals can actively avoid or intensify interactions with other species or individuals (Jeltsch et al., 2013). *Equalizing* and *stabilizing* mechanisms in coexisting species has been shown to be essential for maintaining diversity (Chesson, 2000).

The urge of understanding movement ecology of animals as a driver of biodiversity has been identified (e.g. Jeltsch et al., 2013). Therefore, *movement ecology* has emerged as a new field in ecology that tries to understand spatio-temporal patterns of movement phenomena such as foraging, dispersal and seasonal migration (Nathan and Giuggioli, 2013). Based on the knowledge of animal movement behaviour, conservation and management interventions can be planned to ensure efficient and successful results to maintain and establish biodiversity in ecosystems. So far, links between management planning and knowledge based on movement ecology are rare (but see Allen and Singh, 2016). Conservation and management of wildlife animals require an understanding of "where they are, why they are there, and where else they could be" (Aarts et al., 2008).

Researchers of *movement ecology* aim to find answers to "Where are the animals and why are they there?". Given that the selection of sites has direct effects on fitness (Nathan et al., 2008) and further given, that animals aim to maximize its fitness (McNamara and Houston, 1986), animals are assumed to optimize site selection with respect to the maximization of their fitness (Gaillard et al., 2010). The theory of a reasonably balanced utilization of resources for maximizing the success of survival, growth and reproduction (Charnov, 1976) is generally assumed when analysing site selection. It is assumed, that animals allocate time to a location as a response to conditions present at a site such as resource availability or disturbances. The access and range of conditions vary over temporal and spatial scales. Also, the animal has needs that change over time on different scales, such as energy requirements, need for shelter or search for mating partners. Animals therefore have to cope by adapting site selection to both their current demands and the spatial and temporal distribution of conditions.

Site selection behaviour is analysed in the field of *habitat selection* for more than three decades (e.g. Johnson, 1980; Manly et al., 2002; Aarts et al., 2008). Within this field, researcher aim to understand *why*, *how* and *when* do animals use specific sites. Habitat selection studies try to identify factors that leads to selection or avoidance of sites (Manly et al., 2002). For such studies, typically data on the animal's space use is collected and related to prevailing environmental conditions. The way environmental data is related to space use data, is subject of ongoing discussions in the field of habitat selection (e.g. Keating and Cherry, 2004; Warton and Shepherd, 2010). This thesis is a contribution to the methodology in the field of *habitat selection*.

Habitat selection of animals is driven by a suite of underlying mechanisms, researchers aims to identify. Animals' responses to habitat conditions such as e.g. food availability, degree of cover, predation risk, can be statistically quantified as long these variables are measurable in the landscape. This is usually done in studies of habitat selection (Manly et al., 2002). While movement, the underlying process of habitat selection, is continuous in time (continuous trajectories) this continuous process is discretized into a sequence of locations in the study of habitat selection. Such discrete data capture a series of reflections of the continuous decision-making process of *how* and *why* animals move.

Habitat selection studies try to identify prevailing attributes in the environment of the animals that influence their movement decisions. Environmental attributes and the animals' response may vary over time and may interact with each other. By taking variation and interaction into account, habitat selection studies can provide reliable answers to the question, of *where* and *when* animals move. This thesis illustrates various approaches for quantifying the effects of influencing factors that affect habitat selection of moving animals. Moreover, methods commonly used in economics but rarely or not at all in ecology are adapted to analyse the choice behaviour of animals. These novel approaches provide new perspectives on known concepts in animal (movement) behaviour such as temporal variation, repeatability or functional response.

1.2 Research questions of the thesis

This thesis aims to find and quantify sources of variation in habitat selection by concentrating on large herbivores. Therefore, when addressing the problem of "*How* do animals move?", motion capacity is not referred to. Instead the question of "*Why* and *how* do animals move?" is aimed to be approached by asking "*Where* and *when* do animals move?". Different methodological approaches are presented that are adapted to the particular research question.

This study is conducted in cooperation with the Bavarian Forest National Park. Movement data of free-ranging roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) inhabiting the Bavarian Forest National Park is analysed with respect to environmental conditions. This work provides answers to the question of *where* and *when* animals move and propose suggestions to *why* the animals move.

Even though, the focus is on the methodology, research always starts with questions about the ecological system. The technical implementations merely serve to answer these questions. In particular, our research questions are:

1. **Temporal variation:** Is variation in habitat selection of roe deer over the time of year and time of day related to temporal variation in environmental conditions? (Research paper 1)

2. **Limiting factors on multiple scales:** Finding food or avoiding disturbances - what is the most limiting factor in habitat selection of roe deer? (Research paper 1)

3. **Habitat availability:** How does the availability of a habitat within the home range influence its selection by roe deer? (Research paper 2)

4. **Internal needs vs. availability:** Does habitat use depend more strongly on internal needs or on the availability of a habitat? (Research paper 2)

5. **Repeatability:** How consistent are individuals in their habitat selection behaviour so that natural selection can act upon that behaviour? (Research paper 3)

6. **Individuality:** Does the consistency in behaviour vary between different times of day and between females and males? (Research paper 3)

7. **Individual based movement:** What are the underlying principles in the movement behaviour of individuals that lead to the observed variations in movement and habitat selection patterns on the population level? (Research paper 4)

1.3 Theoretical framework - Concepts and definitions

The movement decision of an animal is a multidimensional process, which researcher aim to understand for more than three decades (e.g. Johnson, 1980; Manly et al., 2002; Aarts et al., 2008). Usually, researcher study the output of the complex process, namely GPS-based recorded positions of animals. Each recording contains the information about the location (x and y coordinate), the time of recording and some other additional information (e.g. temperature, activity), although the latter will not be used in this study. A set of observations of an animal is called trajectory. Trajectories provide pointers of the underlying process and inference to the decision-making process of *where*, *when* and *why* animals move. Thanks to remote sensing of environmental variables, researchers can couple visited location with local conditions. This helps to understand the conditions animal select or avoid.

It is the aim of the researcher to identify the factors that affect movement decisions of animals and to quantify its influence. Due to the great variety of variables influencing habitat selection of animals, researchers need to carefully select the suite of factors to the most essential ones. Some variables are measurable, others such as the internal state of an animal (e.g. hunger, fatigue) are not. However, data would never be sufficient to fully investigate all relevant processes in ecological procedures. Only by simplifying nature to its basic processes, inference on the underlying processes can be made. The pathway to understanding complex systems is simplification (Wissel, 1989).

In the next paragraphs general concepts and definitions in the field of habitat selection are provided.

1.3.1 Resources and habitats

Presence, survival and reproduction of animals within a certain area is determined by the availability of *resources* and *environmental conditions* (Orians and Wittenberger, 1991). Resources are items an individual selects to fulfil its current demands, such as shelter when an animal is freezing or tired, food if it is hungry, water if it is thirsty. Environmental conditions include all abiotic or biotic factors that influences the animal, e.g. weather conditions (e.g. temperature, wind, sunlight, precipitation) or presence of predators or conspecifics. The functional interaction of both resources and environmental conditions defines a *habitat* (Gaillard et al., 2010). This definition has its origin in Hutchinson (1957), who describes the space (niche) in which a species can indefinitely persist as a subset (hypervolume) of a n-dimensional space that is constructed by n environmental variables. In habitat selection studies, models are constructed that are supposed to describe this space with respect to environmental variables.

Availability of resources, like food or shelter, can be measured on a continuous scale. Only if the availability of both resources are independent of each other, one can assume that the axes of the 2-dimensional space are rectangular. In higher space, orthogonality between the axes of n-variables is only ensured if the variables are independent. Certainly, resources in nature are rather entangled and often follow some dynamic gradient which is determined by other environmental conditions or mutually influence each other. For example, biomass and the degree of cover are presumably not independent and therefore highly correlated. Non-detected correlation in statistical analysis can result in wrong conclusions (Dormann et al., 2013). Therefore a variable selection that ensures non-collinearity of factors is necessary in advance when constructing a model.

Variable selection is always a question a researcher is faced with. How can the n-dimensional space Hutchinson is thinking of best described? Technical innovations have been improved and are still improving data acquisition of resource availability and environmental factors to an almost continuous scale in landscape (Cagnacci et al., 2010). But what are the ones that determines animal behaviour the most? In statistics, there is a consensus that the most parsimonious model should be favoured (sensu Occam's Razor[7]) as with increasing number of variables the accuracy of the fit of our data increases but at the same time the applicability of the model prediction for future

[7]The Occam's Razor principle is attributed to the philosopher William of Ockham (1288–1347) which states *Non sunt multiplicanda entia sine necessitate* ("Entities must not be multiplied beyond necessity").

events decreases. This is known as the bias-variance trade-off (Bolker, 2008). Therefore, the researcher is adviced to carefully choose variables included in the model, also with respect to earlier mentioned non-collinearity.

To circumvent variable selection and the resulting problems, *habitat* can also be defined by well distinguishable categories in terms of e.g. vegetation communities (Gaillard et al., 2010). In this case the researcher needs to divide the landscape into a finite sets of discrete habitat units. Such a categorization comes at the cost of describing the landscape from a human-perspective and, of course, involves a simplification of nature (Bunnell and Huggard, 1999; Alldredge and Griswold, 2006).

Both description of habitats, the earlier mentioned functional resource approach and the categorical framework, are legitimated and widely applied in ecological literature (Manly et al., 2002). However, the approaches conceptually differ and makes a direct comparison difficult (Aarts et al., 2012). Though, they complementarily contribute to gain a deeper insight to the mechanism of habitat selection of animals when considering that both frameworks refer to different scales with respect to time and space (Gaillard et al., 2010). The matter of scale was found to play a crucial role in the analysis of habitat selection (Johnson, 1980). The following section will give a brief overview.

1.3.2 The question of scale

The problem of scale is central in ecology (Levin, 1992). Ecological processes occur and, hence, can be analysed on different scales of time and space. Spatial and temporal scales can be considered as hierarchically structured whereby both scales are positive correlated (Delcourt et al., 1982). For instance, roe deer (*Capreolus capreolus*) distribution can be analysed over the whole area of Europe. Analysis of changes over such broad regions make sense rather on a larger temporal scale, such as years, decades or centuries. Dynamics of large-scale roe deer distribution may have been caused by related longer-term changes in vegetational, soil or climatic conditions. Such long-term dynamics in landscape conditions are appropriately observed on a large spatial scale. In contrast, dynamics that influence roe deer distribution in the Bavarian Forest National Park, a small region in Central Europe, may be rather observed on a seasonal, weekly, diurnal or even hourly scale. In order to relate environmental conditions to such small spatial patterns of roe deer distribution, landscape must be characterised on a much smaller spatial scale e.g. in terms of vegetation structure.

Besides the hierarchy and the positive correlation of temporal and spatial scales, scale has two related aspects which are *extent* and *grain*. The extent corresponds to the domain of interest, usually it is the size of study area. The grain is the minimum resolution of the data.

The recognition of the importance of scale greatly influenced the analysis of habitat selection which was initiated by a seminal work by Johnson (1980). According to

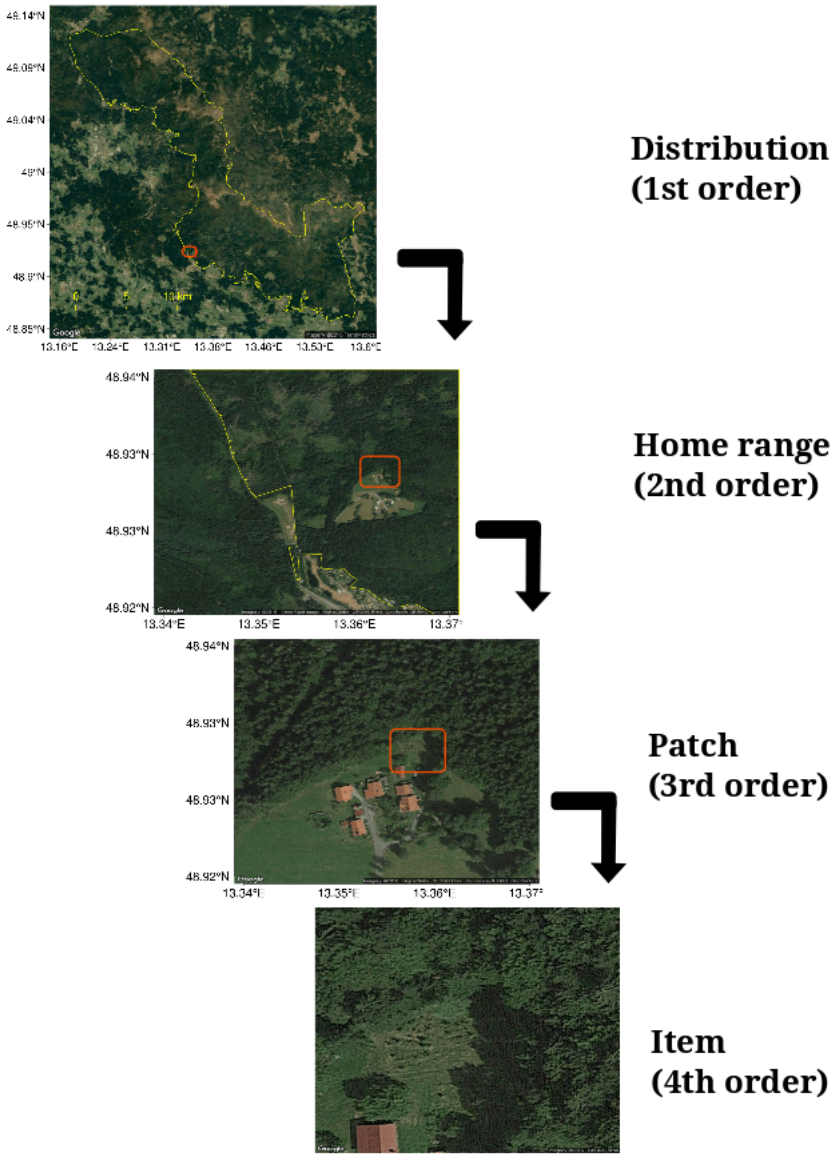


Figure 1.1: The analysis of habitat selection of animals is a matter of scales. Johnson (1980) structured the selection process in four hierarchical levels.

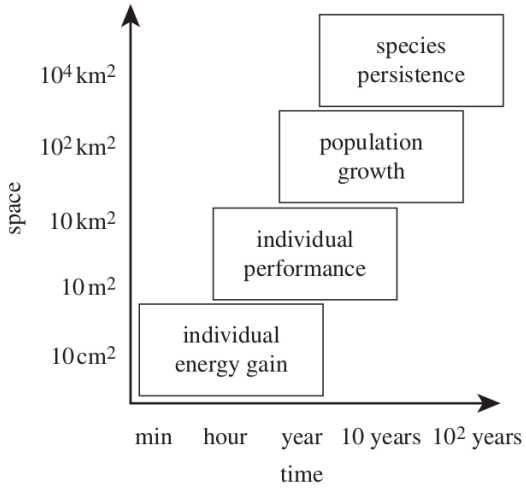


Figure 1.2: Spatial and temporal scales in habitat selection are highly correlated. Data can be provided on high or low resolution on spatial and temporal scale. The resolution of data for an analysis must correspond to the research question. At very small scales the energy intake of an individual can be captured, which would not be possible at broad scales. On this scale, spatial dynamics of a population or species can be studied. (Source: Gaillard et al., 2010)

Johnson (1980) the selection process can be ordered in four hierarchical levels (Fig. 1.1). The *first-order selection* occurs on the largest range, this is the geographical space a species occupy (In Fig. 1.1 it is limited to the study area.). Selection of *second-order* is the choice of home range of an individual or a group within the above mentioned geographical space. *Third-order selection* is the choice of a site within the home range and *fourth-order selection* the actual utilization of an item (resource) at that site. Wiens (1989) adapted the positive correlation of spatial and temporal scales and emphasized that Johnson's spatial levels are directly linked to temporal levels (Fig. 1.2). Hence, the four levels can be transferred to the temporal scale: species persistence > population/individual persistence > feeding/resting period > handling time. This spatio-temporal hierarchy helps to clarify on which level a study intends to provide new insights. It further gives implication of the degree of resolution (grain) the data needs to have to be useful for answering the research question. The resolution of data can vary in time (e.g. time-intervals of GPS-location) and space (e.g. grain size of a map). The optimal scale on which habitat selection should be studied depends on the question the researcher has (Boyce, 2006). If individual behaviour is the scope of the study the resolution of the data needs to be small (Fig. 1.2). If the interest lies in general patterns of the population, resolution can be broader. The question of whether there is an "optimal" scale has not fully answered yet and is related to finding the characteristic scales at which resources most restrictively affect an species' fitness (Mayor et al., 2009).

The recognition of the hierarchical nature of habitat selection and the classification in

different orders by Johnson (1980) helped to analyse and understand the process. Since then, studies on habitat selection are usually conducted on multiple scales (Mayor et al., 2009). Most studies concluded that results can not directly "scaled-up" or "scaled-down" between different scales because of scale-dependent behavioural responses to environmental factors (Bissonette, 1997; Boyce, 2006; Moreau et al., 2012). For example, there has been found non-linear differences in the effect of factors between different scales (Johnson et al., 2002). Consequently, habitat selection on a single scale can not be transferred to another scale. A comprehensive insight can be obtained when analysing habitat selection on multiple scales to define the relevant factors for each scale.

Rettie and Messier (2000) suggested that the factors of different scales also operate hierarchically in habitat selection, whereby factors of larger scales constrain selection on smaller scales. The hierarchy theory is intuitive as habitat selection varies with landscape features that are usually spatially nested in a hierarchical form. For example, climate and geographical conditions constrain landscape features on a very large scale, whereas availability of vegetation types influence habitat selection on a rather small scale. Due to the nested structure of the effects of factors on scales, factors that operate on a large scale are assumed to operate on each successive smaller scale, also. Consequently, limiting factors that affect species' fitness should be avoided at coarse spatial scale, as these operate impairingly on each successive smaller scale. However, Mayor et al. (2009) argued that studies on habitat selection not necessarily support this "top-down" view of selection. Also, a "bottom-up" view is possible, when selection on a small scale entail changes in patterns on large scale.

Concluding, results of habitat selection studies must be interpreted in the light of the focal scale only. A study on multiple scales provide a more comprehensive insight to movement behaviour of the animals. The determination of the scale involves the determination of the extent and grain of the data, e.g. the landscape representation. In the next section the necessity of a sensible choice of the right scale is motivated, as it has direct implications for the definition of availability. The definition of availability, in turn, is related to the evaluation of use and selection.

1.3.3 Clarification of concepts: Availability, use, selection

Availability of resources or habitats, respectively, is a matter of scale (Beyer et al., 2010). In literature one can find several definitions of availability that can be related to Johnson's (1980) scale. For example, availability in habitat selection can be defined based on either the geographic range occupied by a species, the study area, the home range of an individual or even on a single location of an individual (Baasch et al., 2010). As the definition of availability refers to the scale and therefore affects the outcome of a study (Johnson, 1980; Boyce, 2006) the researcher must carefully choose the area of

what is defined as available.

A resource or a habitat, from now on called *unit*, is defined as available to an animal if it has access to it (Lele et al., 2013). The relative *availability* is the proportion of a unit with respect to all available units. Hence, the sum of the proportions of all available units must add up to 1. The *use* of a unit is the proportion of time spent utilizing this unit (Johnson, 1980). The *use distribution* describes the proportion units are used (Lele et al., 2013). A randomly walking animal would use a unit proportionally to its availability (Aarts et al., 2013). However, use is *selective* if the proportion of time spent on the unit is greater or less than its relative availability (Johnson, 1980). It is important to note, that GPS-location data reflects instances of use rather than quantity of use (Lele et al., 2013). However, the more instances are counted for a unit (or conditions on a unit) with respect to the total number of instances the higher gets its weight when calculating the use distribution.

The use distribution depends on the availability of a unit and the *probability of selection* (Lele et al., 2013). The latter is the probability that a unit is selected if it is encountered. Probability of use and probability of selection may strongly differ, if for example an unit is rarely available.

We avoid using the term *preference* in the context of habitat selection, as it originally was defined as selection that occurs under the condition of equal availabilities (Johnson, 1980). Equal availabilities of units in the field is just not realistic and therefore this concept is not permissible in our study.

Study designs differ in the way data is pooled and hence, how availability and use is measured (Thomas and Taylor, 1990). Some studies collect data on the population level with not differentiating between individuals (design 1, Manly et al., 2002). Hence, availability is based on what is present in the study area and equals for all animals and no differences in use between individuals is assumed. Other distinguish between individuals when evaluating use (design 2,3). From those some distinguish between individuals when measuring availability (design 3). Finally, there are studies that measure use and availability for each recording (design 4, Thomas and Taylor, 2006).

In the following applications are presented for for each design.

1.4 Statistical analysis in habitat selection studies

Due to the advent of GPS-based radiotelemetry large datasets on accurate fine-scale relocations of free-ranging animals are available. Those positions represents the interaction of an individual with its environment. Tracking the animal over a longer period of time results in a dataset of recordings, that provides insight to the history of an individual. When multiple individuals are tracked, recorded time-series can be assumed to represent the whole population. When those time-series are related to environmental

data the researcher is able to describe the animals' selection behaviour of landscape characteristics over time and space (with respect to the focal scale, see 1.3.2).

For more than three decades researchers aim to answer the question what shapes habitat selection of animals. There are thousands of studies that try to quantify the effect of abiotic and biotic factors influencing habitat selection of animals. There are several approaches that relate environmental characteristics to animal relocations. Usually characteristics of the used sites are compared with those at available or unused sites. Or the intensity of use is related to landscape characteristics. The statistical analysis of relocation data is diverse (Thomas and Taylor, 2006). In the following the most commonly used approaches are introduced as well as novel approaches used in the publications (chapter 2). But first the much-debated methodological obstacle of autocorrelation in movement data is discussed.

1.4.1 Autocorrelation in movement data

The scale on which the study is wished to be performed determines the frequency with which the positions are recorded. A high frequency of recordings allows a fine-scale analysis where movement trajectories and their characteristics can be inspected. A longer time of recorded positions represents a longer observed period of an animal and allows an analysis on a larger scale like dispersal or migrating behaviour over more than a year (Fryxell et al., 2008). Of course recordings can be easily deleted if frequency is too high, but a high frequency in recording will reduce the overall time period of recording due to limitation in battery life.

However, a high frequency of recordings in animal location data is also associated with a high spatio-temporal autocorrelation (Forester et al., 2007). This is due to the fact that animal movement data originates from a continuous process (Fleming et al., 2015). Spatial autocorrelation implies that sites that are located in close proximity are visited with a similar frequency than expected by chance (Aarts et al., 2008). Temporal autocorrelation increases with a decreasing length of the time interval between successive relocations of an animal. This means that the location at time t is very similar in its attributes to location at time $t-1$ if the length of the time interval is very short.

In the analysis of animal movement data, autocorrelation can both, provide valuable information about the characteristics of movement (Fortin et al., 2005) and negatively interfer the statistics by violating the statistical assumption of independence (Martin et al., 2008).

Within the first case, researchers are interested in the patterns of autocorrelation and aim to identify e.g. movement modes such as searching, foraging or resting behaviour (Fleming et al., 2014). The focus is on the trajectory of an animal which is a path of successive relocations. This path can be characterized by series of step lengths and turning angles. The time series of both metrics can be analysed by measuring the auto-

correlation which may reveal patterns such as periodicity (by autocorrelation functions, Boyce et al., 2010) or seasonal variation in movement behaviour (Cushman et al., 2005). Recent approaches involve variograms that have some statistical advantages over autocorrelation functions (Fleming et al., 2014). But all have in common to use a high temporal resolution to make inference on the dynamic process of movement.

In contrast, habitat selection studies historically analyse movement data in a static way without considering any constraints due to the nature of movement such as navigation and motion capacity of the animals. Researchers usually contrast locations that were selected by the animals against locations that are randomly sampled from the area that is defined to be available to the animal (see section 1.3.3). However, in location data that is highly autocorrelated, two successive locations are very similar in conditions as the animal did not have the chance to relocate to far places. So due to physiological constrains of the animal, it could reach only a small part of the area that is defined as available if the time interval is too short. This violates the assumption underlying most statistical analysis that all randomly sampled locations are equally available. Also, considering the recorded locations of a resting animal that has stayed for a longer time in one place, the multiple recordings of the very same site where it had stayed does not originate from actual selection but is nevertheless compared to the randomly sampled locations from the available area. Therefore, a high autocorrelation is known to increase the probability of type I errors, meaning that the null model of random selection is rejected towards a model that supports specific habitat selection (Martin et al., 2008). Consequently, for the classical approach of hypothesis testing in habitat selection studies (e.g. resource selection functions in section 1.4.3) locations must be independent in time and space (Manly et al., 2002).

To satisfy the assumption of independence or at least to approach it (Rooney et al., 1998), data can be rarified through subsampling. Prior to that, an analysis is needed that identifies the time lag beyond which autocorrelation is sufficiently small. Several approaches have been proposed to identify the so called *time to independence* (TTI, Rooney et al., 1998) such as Schoener's (1981) ratio statistic (Swihart and Slade, 1985) or nonparametric variograms (Fleming et al., 2014). However, subsampling of data means on the one hand discarding redundant information, on the other hand also a loss of ecologically relevant information which may lead to wrong conclusions due to a reduction of biological relevance (Rooney et al., 1998; De Solla et al., 1999). TTI is related to the minimum time an animal needs to cross its entire home range (Rooney et al., 1998). Therefore this approach is only applicable to animals that have a fixed home range (Cushman et al., 2005).

Alternative to subsampling there is a post hoc approach where standard errors, that are underestimated when autocorrelation is present in the data, can be adjusted for (inflated) after the analysis (Nielson et al., 2002).

One more alternative approach is to explicitly modelling autocorrelation by accounting for the serial structure of movement data (Fieberg et al., 2010). Within this approach availability is location specific, which means that also the null model contains spatially correlated locations. One framework, called step selection functions, is explained in section 1.4.5.2 in more detail.

1.4.2 Compositional analysis

In compositional analysis (CA, Aebischer et al., 1993) the proportions of used habitats are compared to the proportion of available habitats. Thereby, animals and not relocations are the sample unit. It can be applied for studies of design 2 and 3, meaning that use enters the model per individual. Availability can be measured either on population (design 2) or individual level (design 3). The designs refer to Johnsons's second and third order selection (see section 1.3.3, Johnson, 1980).

CA provides an order of habitats with respect to their relative preference of selection. However, CA is not appropriate when resource units are described by continuous variables. Unless the variables are categorized in discrete categories.

Despite its wide application in literature, CA in habitat selection studies is not recommended for two reasons (Thomas and Taylor, 2006). First, usually the number of recordings differ between individuals which violates the assumption of a constant covariance structure. Second, a high type I error was reported in several studies if use of a resource is very low (e.g. Pendleton et al., 1998). Due to its popularity the approach of CA is mentioned here. But due to its shortcomings it is not further considered in this thesis.

1.4.3 Resource selection models

Resource selection functions (RSF) using logistic regression models has been the most popular tool to link spatial patterns of animals to landscape characteristics (Duchesne et al., 2010; McLoughlin et al., 2010). Usually, the data for such analysis contains locations where an animal was found (location used) and is compared with available locations (Warton and Aarts, 2013). This is known as *use-availability* design (Manly et al., 2002). Its equivalence to presence/absence, used/unused or case-control designs is shown in Warton and Aarts (2013).

The aim of logistic regression models is to calculate a likelihood that an animal is present at a location, given a set of explaining variables. The response variable y_i is binary, and denotes wether a location i was visited ($y_i = 1$) or not ($y_i = 0$). Each location i is characterized by values of the covariate of dimension J, $\boldsymbol{X}_i = (x_{i1}, x_{i2}, \ldots, x_{iJ})$, which can be continuous or discrete. A resource selection probability function $P(Y_i = 1|x_{i1}, \ldots, x_{ik}) = \pi_i$ is commonly computed using a logistic regression model

with a log link (Manly et al., 2002)

$$\pi(x_i) = \frac{exp(\eta_i)}{1 + exp(\eta_i)},\ \eta_i = \beta_0 + \sum_{j=1}^{J} \beta_j x_{ij} \tag{1.1}$$

where $\eta_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \ldots + \beta_J x_{iJ}$ is the linear predictor function of the explaining variables. The coefficients $\beta = (\beta_0, \beta_1, \ldots, \beta_J)$ are estimated and relate the probability of use to the covariate variables $\boldsymbol{X}_i$. In matrix notation it is $\eta_i = \boldsymbol{X}_i\boldsymbol{\beta}$. The type of environmental variables can be continuous or discrete; quadratic terms or splines can also be used. However, they are assumed to be independent of each other. Its popularity is due to its simplicity in use (McLoughlin et al., 2010). Logistic regression models belong to the family of generalized linear models (GLM, Zuur et al., 2009). GLMs can be extended to generalized linear mixed models (GLMMs) that can account for heterogeneity and dependency in the response variable. In the context of habitat selection it is advisable to use GLMMs to consider e.g. variation between individuals due to individuality or differences in landscape conditions or different samplings (Gillies et al., 2006). In this case the linear predictor is extend to

$$\eta_i = \boldsymbol{X}_i\boldsymbol{\beta} + \boldsymbol{Z}_i\boldsymbol{b}_i,\ \boldsymbol{b}_i \sim N(\boldsymbol{0}, \boldsymbol{D}) \tag{1.2}$$

where $\boldsymbol{b}_i$ is a random vector that contains random effects, with zero expected value and covariance matrix $\boldsymbol{D}$, $\boldsymbol{Z}_i$ is the model matrix for the random effects. In habitat selection studies random effects can be for example the id of individuals, that allows some degree of heterogeneity among individuals and account for non-independence in habitat selection behaviour within the individuals, respectively. Or random effects can include the different study sites, that account for not specified differences. Also, possible effects of the time of data recording can be included by adding a random effect of time in the model. In general, random effects are reasonable to be included, if differences between units (e.g. animals) are likely, and the degree of difference per unit is of no interest. As the covariance matrix $\boldsymbol{D}$ is estimated one can quantify the variability in habitat selection that is due to the differences between units.

Logistic regression in habitat selection studies has due to its simplicity and flexibility many advantages. But it has also some well known problems, which are thoroughly discussed in literature. Most problems are related to the choice of points that are designated to be available ($y_i = 0$, e.g. Phillips et al., 2009; Hastie and Fithian, 2013; Warton and Shepherd, 2010; Warton and Aarts, 2013). Three problems are illustrated in Fig. 1.3. First, the problem of *implementation*: the way the available points (or "pseudo-absences") are generated are known to influence the model outcome and accuracy. Preference or avoidance of a habitat can vary for different definitions of what

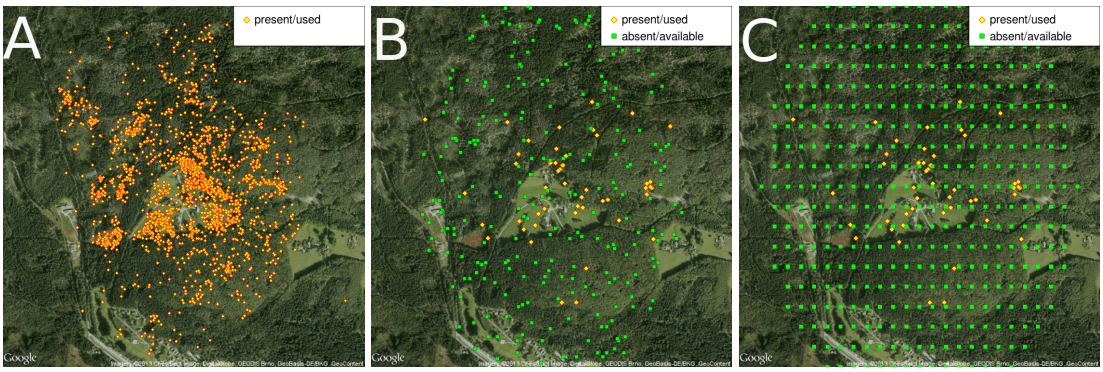


Figure 1.3: GPS-based recordings of positions (yellow) of a male adult roe deer in the Bavarian Forest National Park. Figure A shows all positions ever recorded for this individual. Figures B and C show only a subset of those, which is what the researcher usually has acquired. Green points present possible generated available points. In contrast to figure A it is obvious that green points are "pseudo-absence" points and are designed for representing the conditions in the landscape. Figures B and C demonstrate that the way "pseudo-absence" points are generated can influence the outcome of a model, as the availability of conditions may differ between B and C.

is available to the animal (Beyer et al., 2010). Here, the researcher needs also to be aware of the scale problematic (see section 1.3.2). The method of the generation of random points affect the model's predictive accuracy, so that it is recommended to sample a large number of pseudo-absence points (Barbet-Massin et al., 2012). Second, the problem of *interpretation*: estimated probabilities, also called "relative probabilities" (Manly et al., 2002), depends on the number of "pseudo-absences" (Warton and Shepherd, 2010) and are not necessarily proportional to probability of use (Keating and Cherry, 2004). Third, the problem of *contamination*: in particular for mobile animals one can not ensure that randomly chosen "pseudo-absences" have never been used. Such "contaminated" controls are found to bias the estimation of model coefficients to a more or less great extent when applying standard logistic regression (Rota et al., 2013). The root of all potential problems lies in the more or less arbitrary researchers' choices for generating new data or "pseudo-absence" points.

All mentioned problems can certainly be issues when analysing movement data of animals. But if the researcher is aware of all this, sensibly ponders optional approaches, if decisions are reasonable and based on the research question, RSFs are a very useful tool to analyse habitat selection of animals (Warton and Aarts, 2013).

1.4.4 Poisson point process models

Observed locations can also be analysed as the events of a spatial *Poisson point process* (PPP). Properties of a PPP with intensity $\lambda > 0$ in a two-dimensional region $\mathcal{B}$ are

(i) **Poisson distributed number of points:** the number of of points y falling in

any region $B \subset \mathcal{B}$ is a Poisson random variable; $Pois(y|\lambda) = \frac{e^{-\lambda}\lambda^y}{y!}$

(ii) **Independence:** if $B_1 \subset \mathcal{B}$ and $B_2 \subset \mathcal{B}$ are disjoint sets then the number of points y_{B_1} and y_{B_2} are independent random variables.

λ can be interpreted as the mean density of points in region $\mathcal{B}$. In a homogeneous PPP the points are uniformly distributed in space. Hence, for a homogeneous PPP the expected number of points falling in $B \subset \mathcal{B}$ is $\mathbb{E}[y_B] = \lambda \cdot area(B)$. This means that the number of visits in a subregion is related to its area in region $\mathcal{B}$, hence, more visits are predicted in larger regions. This area-occurrence-relation would be expected from a randomly walking animal. However, in ecology the animal is assumed to optimize resource selection. Hence, an animal is expected to visit those places more often that maximizes its fitness. Therefore, to gain an understanding of what drives habitat selection of animals, the number of occurrences y_i in habitat (or region or location) i is related to environmental covariates. This can be done with assuming a inhomogeneous PPP model with a log-linear link function:

$$log(y_i) = \beta_0 + \sum_{j=1}^{J} \beta_j x_{ij} = \boldsymbol{X}_i\boldsymbol{\beta} \tag{1.3}$$

Also, quadratic effects or splines, as well as random effects can be included. If the area differ between the categories or regions the logarithm of value of the area must be included as an offset.

Such models rely on observed data only and do not need "pseudo-absences". Warton and Shepherd (2010) showed that under certain circumstances a logistic regression model is asymptotically equivalent to a PPP model (PPM). They further clarify that PPMs have natural solutions to all formerly mentioned issues of implementation, interpretation and contamination (section 1.4.3). But there is one mathematical caveat. PPMs for animal location data assume that the total number of recordings is unknown, which is not correct. Indeed, as the number is known, the to be estimated intensities of presences are not independent, which means that the count data is multinomial. An alternative is a surrogate Poisson model that accounts for the multinomial structure of the data (Venables and Ripley, 2002).

Let y_i be the intensity of selection of habitat type i, a_i is the area of i, then the surrogate Poisson model is written as an extension of equation 1.3:

$$\log(\lambda_j) \sim \prod_r \boldsymbol{\delta}_r \boldsymbol{M}_r + \log(a_i) + \boldsymbol{X}_i\boldsymbol{\beta} + + \boldsymbol{Z}\boldsymbol{b},\ \boldsymbol{b} \sim N(\boldsymbol{0}, \boldsymbol{D}) \tag{1.4}$$

where $\boldsymbol{b}$ is a random vector that contains random effects, with zero expected value and covariance matrix $\boldsymbol{D}$, $\boldsymbol{Z}$ is the model matrix for the random effects. The first term $\prod_r \boldsymbol{\delta}_r \boldsymbol{M}_r$ refers to the multinomial structure of the data. It is the product of

all factors for which a classification is wished and the counts refer to e.g. counts per habitats and sex and age. These extra parameters must also be estimated. For the example habitats per sex, it would mean $2K$ extra parameters for K habitats and 2 sex categories. Hence, due to fitting this extra parameter, surrogate Poisson models imply a high computational effort. Consequently, this approach is only feasible for a low number of categories. The advantage of this approach is, that the model is easy to implement as software is established for Poisson models. So, surrogate Poisson models present a possible way to estimate multinomial models with a possibly high computational burden. For models with a high dimension of categories, discrete-choice models may be the better alternative. However, for discrete-choice models easy-to-use software is not available yet, especially not when random effects are supposed to be included.

1.4.5 Discrete-choice models

If an animal is assumed to choose from a discrete set of options, e.g. habitat types or specific patches, the choice can be modelled with discrete-choice models (Agresti, 2002). The response variable consists of a discrete set of alternatives. Explanatory variables that are supposed to explain the choice behaviour of the animals can be of two types: *i*) characteristics of the alternatives and *ii*) characteristics of the chooser. In the first case, the alternative, e.g. the habitat, is described by its properties, such as availability of food and cover or its value for the animal. McFadden (1974) proposed this type of model as a *conditional logit* model[8]. In the second case, properties of the chooser, namely the animal are included that may influence habitat selection such as sex or age. It is possible to include both types of variables in discrete-choice models (see pp. 313f in Agresti, 2002, for the derivation).

If the number of alternatives is two, the response variable is dichotomous or binary, otherwise it is called polytomous or multicategory. In the first case GLMs with a binomial distribution can be used as explained in paragraph 1.4.3 (about RSFs). In the case of a polytomous or multicategory variable discrete-choice models should be analysed using multinomial models, which is the scope of the next two paragraphs.

Discrete-choice models are widely used in social science and economics for modeling a subject's choice from one of several discrete alternatives. Despite the apparent similarity of the problems discrete-choice models are rarely used in studying habitat selection (Vergara Cardozo et al., 2010). One reason for disregarding the multinomial structure of the data might be the lack of adaptable software tools (but see Duchesne et al.,

[8] McFadden (1974) called this type of model *conditional logit* since the influence of a variable on the choice depends on the difference of the variable's values for the choices. If there is no difference, the model reveals no effect of the variable on the choice. In 2000, McFadden received the Nobel Prize "for his development of theory and methods for analyzing discrete choice".

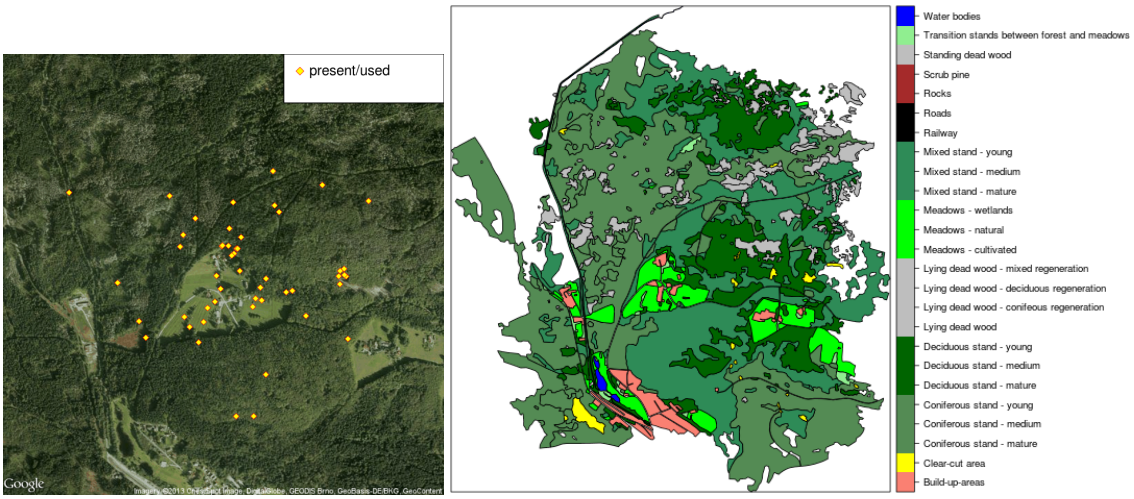


Figure 1.4: The same extraxt of landscape of the Bavarian Forest National Park (see Figs. 1.1 and 1.3 B) showing the landscape photographed by a satelite (left) and represented as an area built up by well-defined categorical habitat types.

2010; Craiu et al., 2011). An alternative present surrogate Poisson models (see section 1.4.4), which however are computationally intensive if the number of alternatives is too high.

In discrete choice models the probability of choosing a subject i is conditional on the choice set C_t at time t. Each item i in the choice set is characterised by J explanatory variables $\boldsymbol{x}_{ti} = (x_{ti1}, \ldots, x_{tiJ})'$, and let $\boldsymbol{x}_t = (\boldsymbol{x}_{t1}, \ldots, \boldsymbol{x}_{tJ})$. The probability of selecting option i at time t is

$$\pi_i(\boldsymbol{x_t}) = \frac{\omega(\boldsymbol{\beta}, \boldsymbol{x_{ti}})}{\sum_{h \in C_t} \omega(\boldsymbol{\beta}, \boldsymbol{x_{th}})} \tag{1.5}$$

where $\omega(\boldsymbol{\beta}, \boldsymbol{x})$ is some functional form of covariates $\boldsymbol{x}$ and coefficients $\boldsymbol{\beta}$. $\omega(\boldsymbol{\beta}, \boldsymbol{x})$ can be regarded as a form of resource selection function, e.g. as η_i in equation 1.1. Smooth effects of the variables and random effects can be included to account for flexible forms and multiple sources of variations in habitat selection. Also, characteristics of the animal (e.g. age or sex) can be included (Agresti, 2002). Equation 1.5 ensures that the sum of probabilities over the choice set C_t equals 1. Discrete choice models were found to provide the most accurate and precise estimate of coefficients in a simulation study about habitat selection (Baasch et al., 2010). There are different ways of applications. If the strength of selection of patches in a categorised landscape is the aim of the study (Fig. 1.4), baseline-category logit models are appropriate. If one is interested in the effect of specific variables on site selection, step selection functions are recommended.

1.4.5.1 Baseline-category logit models

Given an animal that has the choice out of $i = 1, \ldots, K$ habitats, one can calculate the probability π_i of choosing habitat i. As there are exact K choices the probabilities must sum to 1, $\sum_i \pi_i = 1$.

Multinomial logit models with a multicategory response can be fitted using baseline-category logit models (Agresti, 2002). The baseline category should be the most commonly selected category. Given the multinomial structure of the model, the probability of choosing the baseline category K is calculated as: $\pi_K(\boldsymbol{x}) = 1 - \pi_1(\boldsymbol{x}) - \ldots - \pi_{K-1}(\boldsymbol{x})$, where $\boldsymbol{x}$ is a vector of covariates describing the habitat and/or the individual. Probabilities $\pi_i(\boldsymbol{x})$, $i = 1, \ldots, K-1$ are derived by first fitting $K-1$ binary logit models separately to the data. In this first step the response variable of $K-1$ models is now binary ($y \in \{0, 1\}$) and logistic regression is performed as shown in equation 1.1. The ith model include observations from habitat i and K only, where $y = 1$ if individual was observed in habitat i and $y = 0$ if it was observed in the reference habitat K. Given $f_i(x)$, the selection ratio calculated from the logistic regression that contrasts the selection between habitat i and the reference type K, probability of selection of habitat i is estimated via the multinomial logit link:

$$\pi_i(\boldsymbol{x}) = \frac{exp(f_i(\boldsymbol{x}))}{1 + \sum_{s=1}^{K-1} exp(f_s(\boldsymbol{x}))} \tag{1.6}$$

with f_i being a general functional form of the explanatory variables that can be habitat-specific. f_K is 0 for identifiability reasons. The denominator of equation 1.6 is the same for all i. Explanatory variables $\boldsymbol{x}$ can be continuous or discrete, characterising the focal habitat i or properties of the individual.

Multinomial logit models have rarely been used in habitat selection studies, but see very simple versions (Arthur et al., 1996; McCracken et al., 1998; Cooper and Millspaugh, 1999; McDonald et al., 2006), despite the suite of advantages (Kneib et al., 2011). For example, these models do not suffer from the in section 1.4.3 mentioned issues of implementation, interpretation and contamination as these do not need "pseudo-absences". These models are based on observed data only. Furthermore, availability of habitats can be included for each individual. The model formulation is highly flexible, as the model can be formulated for each habitat separately. So that, for example, effects of covariates can vary among habitats and over time. Random effects that account for variation among individuals can also be integrated.

Another positive aspect of multinomial logit models over RSF is that it does not implicitly assume the independence from irrelevant alternatives (IIA) as studies with RSF usually do (Duchesne et al., 2010). The hypothesis of IIA postulates that the selection of a certain habitat over another is independent of the availability of other

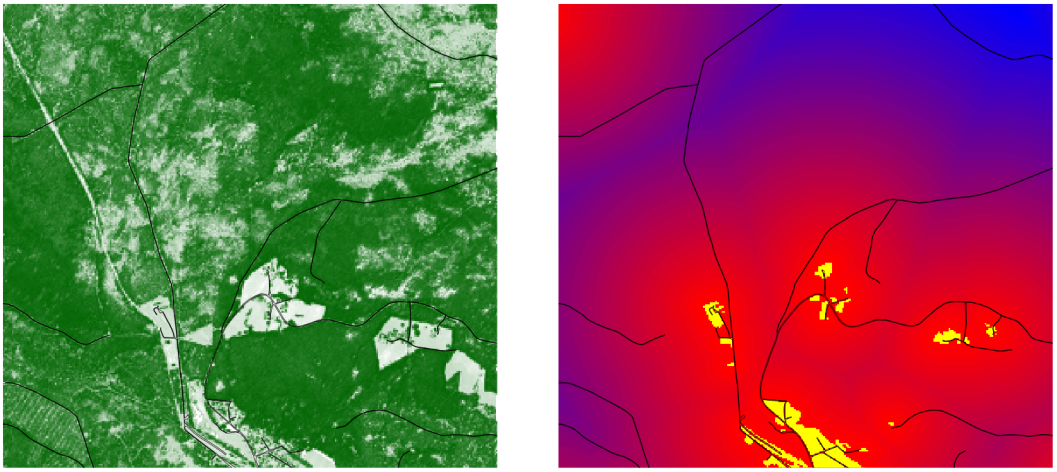


Figure 1.5: Landscape (same extraxt of landscape of the Bavarian Forest National Park as in Figs. 1.1, 1.3 and 1.4) presented as a landscape of continuous variables. The left figure shows the landscape according to the degree of canopy cover in summer, the darker the higher the degree of cover. Black lines are roads. The right figure visualizes the distance to settlements (yellow).

habitats. In multicategory logit models the probability of selecting a certain habitat is conditional on the selection of all other habitat available to an individual (equation 1.6). Hence, the IIA is not assumed.

However, the analysis of habitat selection with multinomial logit models requires a discretization of the landscape into categories. This may be an improper simplification of nature. An alternative is to analyse how variables influence the selection of animals. The analysis can be achieved by using step selection functions.

1.4.5.2 Step selection function

Another form of multinomial model is the conditional logit model, where the choice is modelled as a function of the characteristics of the alternatives, e.g. percentage of cover, availability of food or distance to settlements (Fig. 1.5). Conditional logit models are usually applied in the context of step selection function (SSF, Thurfjell et al., 2014). It is a rather new approach (Fortin et al., 2005) that has started to become more and more applied. SSF analysis is structurally a RSF analysis of design 3 and 4 and refers to Johnson's third and fourth order selection. It allows to analyse data on a very fine spatio-temporal scale. In SSF a series of animal relocations is analysed. The set of available alternatives (C_t) is defined stepwise. Within a step the actual chosen location is compared with locations that might have been chosen out of the direct surrounding of the last step. So, the data consists of location data of the animal, where each visited

location is matched with a set of randomly chosen points. These random points are usually sampled given the last position and a step length and a turning angle. The last two are randomly sampled from some distributions of step lengths and turning angles commonly obtained from other monitored animals (Fortin et al., 2005).

The fix rate, which is the frequency of sampling, determines the spatio-temporal scale. Again, as stated in section 1.3.2, the resolution depends on the research question (Thurfjell et al., 2014).

Structurally, SSF belong to *discrete choice models*. Given the matched (or case-control) design of the data, a conditional logistic regression is needed to appropriately analyse the data (Fortin et al., 2005). By doing this some of the earlier mentioned problems in RSF (section 1.4.3) are encompassed. Clearly, the problem of "implementation" is still a decision the researcher has to made, but the influence is less than in RSFs as the estimates are conditioned within the strata (Thurfjell et al., 2014). The risk of "contamination" due to actually used sites is very small for a high temporal resolution, albeit, increases with a lower temporal resolution. However, the problem of interpretation remains as the estimated coefficients are calculated on a latent scale (which is connected to probability via a link function which is conditioned within the strata).

The IIA is assumed in standard conditional logit models (McFadden, 1974), where only attributes of the choices are included as fixed effects. However, if random effects are added in equation 1.5 the assumption of IIA is attenuated on the levels of the random effects, as changes of a variable influences the choice differently (Duchesne et al., 2010). For example, the addition of a random effect for the individuals allows heterogeneity on the population level and correlation of the choices within an individual, respectively. Duchesne et al. (2010) shows that in case of a mixed multinomial logit model the choice of a habitat depends on the local alternatives.

1.5 Individual-based movement models

A fundamental understanding of animal movement will help to predict species occurrence under changing global conditions. Approaches in the field of movement ecology are diverse. Within the well established resource selection studies (RSF), selection of habitats is analysed, given the relative availability and use of particular habitats. Introduced during the 1970s (Manly, 1974), RSF have been intensively applied during the last decades (Thomas and Taylor, 1990, 2006; Arthur et al., 1996; Aarts et al., 2008; Forester et al., 2009). The relative use of resources is statistically compared with the relative availability by applying a form of logistic regression. The fit of such analysis provides a quantification of the strength of the selection of habitats or environmental conditions. RSF studies can offer an insight into the ecology of animals (Arthur et al., 1996; Godvik et al., 2009; Duchesne et al., 2010) and help to answer the ques-

tion of "How and why do animals move". Inference from such studies can also be used for evaluating management and conservation activities (Chetkiewicz and Boyce, 2009). However, caution is needed in making inference from such models. Earlier studies reveal the limits of the habitat selection design and argue that estimates of preference may be prone to misleading interpretation (Keating and Cherry, 2004). Further, it is vague whether such studies provide a reflection of the internal demands of animals (Keating and Cherry, 2004; Beyer et al., 2010).

Individual-based movement models (IBMM) focus on the individual. The decision making process of an individual at potentially small temporal and spatial scales is the focus of IBMMs. The individual is the "building block" (Grimm and Railsback, 2005) of a greater system and allows therefore inference on patterns of higher hierarchical levels, such as population level. IBMMs have become very popular in movement ecology (Jonsen et al., 2005; Schick et al., 2008). Its framework include a hypothetical mechanistic model (process model), which contains the movement rules, and an observation model, which links the process model to data. The basic structure of the process model is Markovian, meaning that the state, here the location, in the next time step only depends on the current state/location (processes of higher order are also practical). The transition from one location to the next is controlled by the transition state equation, which contains the drivers of movement in focus. Drivers might be movement metrics like step length and turning angle (e.g. correlated random walk, Franke et al., 2006; Johnson et al., 2008; Gurarie et al., 2009, see an animation in the electronic appendix), the attractivity or repulsion of landscape features (e.g. biased correlated random walk, Avgar et al., 2013; Moorcroft et al., 2006) or both (Morales et al., 2004; Forester et al., 2007). Drivers of movement are included as covariates in the transition state equation. Its strength and the direction of its effect on the movement decision is determined by parameters. The framework of IBMMs permits the parameters to change according to different behaviorial modes such as resting or foraging. This allows the modeller to set up a ecologically meaningful model.

A fundamental problem of IBMs is the verification of validation. An option is inverse modelling (Latombe et al., 2011). An IBMs is a bottom-up model, meaning that processes on a lower level (individual-level) are modelled to analyse general principles on higher hierarchical levels (population level, Grimm et al., 2005). Hence, the modeller aims to understand patterns found on the population level with generating mechanisms modelled on the individual level (e.g. home range size, Van Moorter et al., 2009). The model can be evaluated by its ability to reproduce patterns when it is used to simulate new data. This begs the question of how complex must the model be to capture the behaviour and structure of a real system sufficiently well? Grimm et al. (2005) recommend to use not only one but multiple patterns observed in nature to validate the model. If a model is used to reproduce only one pattern, it probably lacks structural realism.

For example, Van Moorter et al. (2009) was able to reproduce realistic home ranges with a mechanistic movement model based on a biased correlated random walk. The model includes rules that describe geometric characteristics of movement, only, such as directional persistence, step length or memory. Hence, it was built for the purpose of generating home ranges, but, this model is not useful in gaining knowledge about the underlying drivers of animal movement. Consequently, to ensure that the model captures essential mechanisms of a movement, multiple patterns should be used to validate the model (Grimm et al., 2005). However, if there are too many patterns, the complex design and analysis of the model may involve a disproportionate effort. Therefore, Grimm et al. (2005) proclaimed the pattern-oriented modelling (POM) approach to find the optimal complexity of a model. The development of an IBM using POM involves five tasks: i) define the problem, ii) acquire theories, iii) choose model structure, iv) implement the model, v) analyze the model (Grimm and Railsback, 2005). These steps have to run through several times until the test-patterns can be adequately reproduced by the individual-based simulation. Latombe et al. (2011) suggest to include one more task between the third and the fourth point, which is model parametrization. A forward modelling approach at this stage would simplify the parametrization using POM as it shortens the parameters' refinement process. Latombe et al. (2014) combined a SSF approach with an IBM that integrated internal states such as stored energy and a representation of the memory of visited locations. They were able to capture complex patterns in the movement ecology of caribou (*Rangifer tarandus caribou*) with respect to habitat selection and home range sizes.

The flexibility and the high complexity of IBMs usually entail computationally expensive statistical methods to estimate parameter distributions (Patterson et al., 2008) such as Bayesian Monte Carlo methods. Even though there exist convenient software that afford very little additional programming effort (Lunn et al., 2009) computational time can be extremely long when parameter space and/or data sets are large. This is even aggravated if the number of behaviorial modes is unknown (McClintock et al., 2012).

In the past, conceptual individual-based movement models have provided links between individual behaviour and space use patterns like site fidelity (Fronhofer et al., 2012; Van Moorter et al., 2009; Mueller and Fagan, 2008; Berger-Tal and Avgar, 2012; Gautestad, 2011). But mechanistics used in such models are not easily transferable to models that aim to reproduce empirical data. Especially cognitive abilities can not be measured and its effect on movement decision is rather vague (Dalziel et al., 2008) and can be estimated only indirectly (Avgar et al., 2013; Gautestad et al., 2013). However, models that integrated internal states such as stored energy and a representation of the memory of visited locations were able to capture complex patterns in the movement ecology of caribou (*Rangifer tarandus caribou*, Latombe et al., 2014).

1.6 Study system

1.6.1 The area – Bavarian Forest National Park

The Bavarian Forest National Park is situated in south-eastern Germany along the border to the Czech Republic ($49\,°30'19''N, 13\,°12'9''E$). Together with the Sumava (Bohemian Forest) National Park they built up the largest protected area of forest remainig in central Europe. Since its establishment in 1970 its managment philosophy is "Let nature be nature" resulting in a large landscape of wild forests and bogs. On its total area of 24,218 ha, 3,850 animal species have been identified.

Spectrozonal aerial images of the study area from 2008 (Heurich et al., 2012) were used to classify forest areas according to the land cover (Belyaev et al., 2004). Images with a resolution of 0.4 m were used to isolate vegetation against the background of other underlying surfaces, different kinds of vegetation and different stages of vegetation of the same species (Belyaev et al., 2004). This resulted in a categorization of the landscape in 25 land-cover classes (Fig. 1.5).

The national park has three major forest types. Above 1,100 m a.s.l. (16% of the area), sub-alpine spruce forests of Norway spruce (*Picea abies*) and some mountain ash (*Sorbus aucuparia*) prevail. On the slopes between 600 m and 1,100 m a.s.l., mixed montane forests with Norway spruce, white fir (*Abies alba*), European beech (*Fagus sylvatica*) and sycamore maple (*Acer pseudoplatanus*) (68% of the area) are found. In wet depressions in the bottom valleys (16% of the area), often associated with cold air pockets, spruce forests prevail with Norway spruce, mountain ash and birch (*Betula pendula, Betula pubescens*) (Heurich and Neufanger, 2005). Since the mid-1990s, the forests of the national park have been affected by massive proliferation of the spruce bark beetle (*Ips typographus*). By 2011, this had resulted in the death of mature spruce stands over an area amounting to about 6,000 ha (Heurich et al., 2010; Lausch et al., 2010). Management of roe deer in the national park is spatially limited to the wild ungulate management zone. This management zone comprises approximately 20% of the study area and serves as a buffer zone in the transition area to the landscape surrounding the national park. This ensures that wildlife regulation measures are excluded from a core area of 20,000 ha (Heurich et al., 2011). The estimated roe deer population density was 1-3 animals/km^2 (M. Heurich, unpublished data). During our study, roe deer in the national park were subjected to predation by European lynx (*Lynx lynx*) which had been reintroduced in the 1980s (Wölfl et al., 2001).

For our study we aggregated the 25 land-cover classes to meaningful habitat types with respect to roe deer ecology (Fig. 1.6). Medium aged stands are characterised by a natural undergrowth, and hence, provide cover and food of high quality. For deciduous stands great changes occur in conditions on the seasonal scale. In winter due to snow, there is hardly any food and no cover, in spring undergrowth supplies much highly

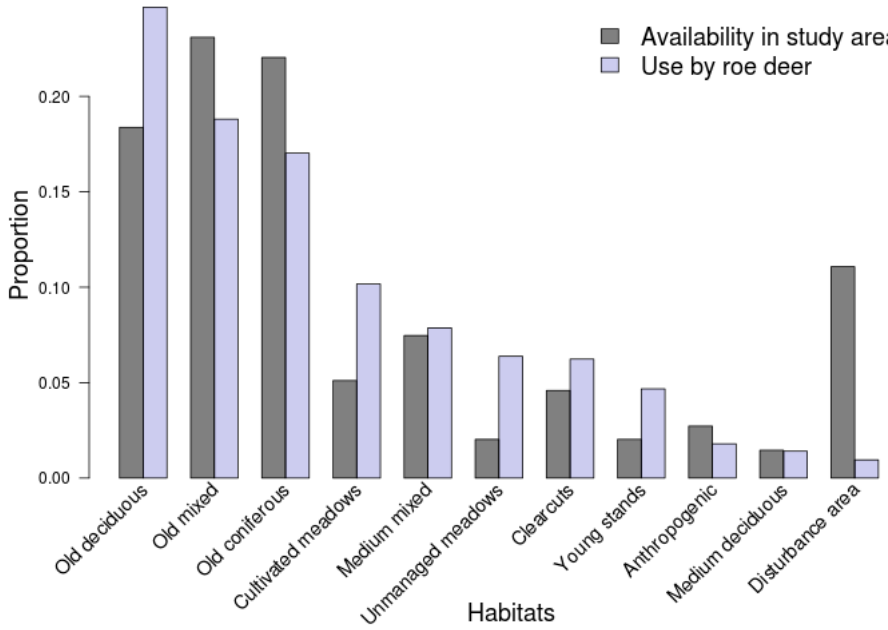


Figure 1.6: Percentual availability of habitats in the study area Bavarian Forest National Park, Germany (grey bars) contrasted with the percentual use of habitats by roe deer (blue bars).

nutritious food (Marell et al., 2009). In autumn, high-energy beechnuts are provided (Olesen and Madsen, 2008). Undergrowth from spring to autumn also provide optimal hunting conditions for lynx (Lone et al., 2014). Mature stands have sparse undergrowth, providing low forage and cover. Low cover is connected to low predation risk by lynx. Open habitats such as anthropogenic area and cultivated meadows, provide much food of high quality. However, open areas provide no shelter from human disturbances, but optimal visibility to avoid predation by lynx. Unmanaged meadows and young stands provide both, much high-quality food and high cover. High cover results in optimal shelter from humans, but simultanously in optimal hunting conditions for lynx and therefore in a higher predation risk. The opening of the forest canopy in clearcut areas results in a stronger growth of ground vegetation and therefore plenty of highly nutritious food. These sites, however, provide hardly any cover, which reduces predation risk by lynx but also shelter from human. Bark beetle areas, characterised by lying dead wood and natural undergrowth, provide a good amount of high-quality food in summer. Lying trunks and branches provide optimal hunting conditions for lynx.

1.6.2 The species – roe deer

A considerable plasticity in the habitat selection of European roe deer has been observed but not fully understood (Morellet et al., 2011). Roe deer live in woods but are also

widely distributed in fragmented and more open agricultural areas (Hewison et al., 2001). Roe deer are strongly attached to their home ranges and occupy the same site for many years (Linnel and Andersen, 1995). Their habitat use has been intensively studied, and effects of habitat features on some life-history traits have been detected (Pettorelli et al., 2003; Nilsen et al., 2004). Many studies on the spatial behaviour of roe deer have differentiated between the sexes. Significant differences in spatio-temporal behaviour between females and males have been reported, e.g. time-budgeting (Turner, 1979), home range size (Cederlund, 1983), patterns in home range occupation (Bideau et al., 1993), spatial displacement after capturing (Morellet et al., 2009), and residence time in the summer range (Cagnacci et al., 2011). The results indicate that it is reasonable to distinguish between the sexes in the analysis of roe deer habitat use. Despite the vast number of studies of the use of space by roe deer, only little is known about the rules governing roe deer habitat selection (Coulon et al., 2008), including preference and avoidance of areas. Certain habitat types are visited more frequently than others relative to their proportional availability (Tufto et al., 1996; Morellet and Guibert, 1999). There are strong hints that roe deer behaviour changes monthly and diurnally (Turner, 1978; Cederlund, 1989; Pettorelli et al., 2005; Le Corre et al., 2008) and the composition of the roe deer diet varies seasonally (Cornelis et al., 1999). However, studies on the variation in resource selection by roe deer have either not taken the temporal scale into account or only considered a coarse temporal scale, such as day/night or season (Mysterud et al., 1999; Morellet et al., 2011).

The roe deer is a highly concentrate feeder, which, combined with its relatively small size make it particularly dependent on food quality. Because of its direct effect on mortality and the sub-optimal use of habitats to minimize predation risk by prey species, predation is generally regarded as the main factor limiting the fitness of large herbivores (Lima and Dill, 1990).

Chapter 2

Research Papers

Contents

Research paper I

Title	Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources
Authors	Claudia Dupke, Christophe Bonenfant, Björn Reineking, Robert Hable, Thorsten Zeppenfeld, Michael Ewald, Marco Heurich
Status	published 2016 in Ecography (in press)

Own contribution: concept and study design 75%, statistical analysis and presentation 100%, conception and writing the manuscript 80%
The study was designed as a cooperation by CB, CD, BR and MH. MH, ME and TZ acquired and processed field data. BR and RH gave advice in the statistical analysis. CB, CD and MH wrote the manuscript. All authors revised the manuscript.
CD is the corresponding author.

Research paper II

Title	Shape of functional response reveals strength of trade-off in resource use by a large herbivore
Authors	Claudia Dupke, Marco Heurich, Björn Reineking, Christophe Bonenfant
Status	in preparation

Own contribution: concept and study design 80%, statistical analysis and presentation 100%, conception and writing the manuscript 90%
The study was designed by CB, CD, BR and MH. MH provided field data. CB and CD wrote the manuscript. All authors revised the manuscript.
CD is the corresponding author.

Research paper III

Title	Quantifcation of repeatability in habitat selection behaviour
Authors	Claudia Dupke, Christophe Bonenfant, Marco Heurich, Björn Reineking
Status	submitted to Methods in Ecology and Evolution

Own contribution: concept and study design 70%, statistical analysis and presentation 95%, conception and writing the manuscript 70%

The study was designed by CB, CD, BR and MH. MH provided field data. BR gave advice in the statistical analysis. CB, CD and BR wrote the manuscript. All authors revised the manuscript.
CD is the corresponding author.

Research paper IV

Title	On the move: Modelling habitat selection of large herbivores
Authors	Claudia Dupke, Florian Hartig, Marco Heurich, Björn Reineking
Status	in preparation

Own contribution: concept and study design 80%, model design and implementation 95%, conception and writing the manuscript 100%
The study was designed by CD, BR, FH and MH. MH provided field data. FH and BR gave advice in the modelling process. CD wrote the manuscript.
CD is the corresponding author.

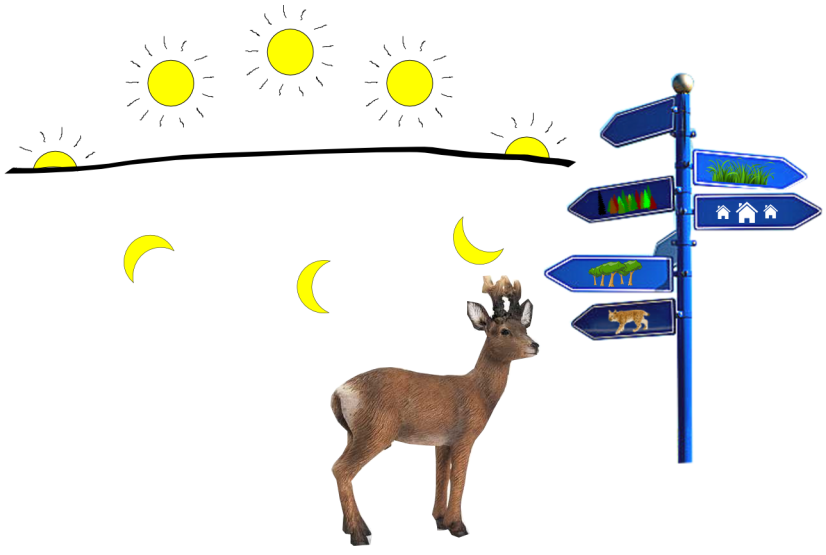
Research paper I

Claudia Dupke, Christophe Bonenfant, Björn Reineking, Robert Hable, Thorsten Zeppenfeld, Michael Ewald, Marco Heurich

Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources

Ecography, 2016 (in press)
10.1111/ecog.02152

Summary: Variation in habitat selection is related to seasonal plant phenology and human disturbances and not to lynx predation risk on the focal spatial and temporal scales.



Authors affiliation:

Claudia Dupke*[1], Christophe Bonenfant[2], Björn Reineking[1,3], Robert Hable[4], Thorsten Zeppenfeld[5], Michael Ewald[6], Marco Heurich[7,8]

[1] Biogeographical Modelling, Bayreuth Center of Ecology and Environmental Research BayCEER, University of Bayreuth, Universitätsstr. 30, 95440 Bayreuth, Germany

[2] Université de Lyon, F-69000, Lyon, Université Lyon 1, CNRS, UMR5558, Laboratoire de Biométrie et Biologie Évolutive, F-69622, Villeurbanne, France

[3] Université Grenoble Alpes, Irstea, UR EMGR 2 rue de la Papeterie BP 76, 38402 St-Martin-d'Héres, France

[4] Department of Mathematics, University of Bayreuth, Universitätsstr. 30, 95440 Bayreuth, Germany

[5] Department of Landscape Ecology, University of Göttingen, Goldschmidtstr. 5, 37077 Göttingen, Germany

[6] Institute of Geography and Geoecology, Karlsruhe Institute of Technology, Kaiserstr. 12, 76131 Karlsruhe, Germany

[7] Chair of Wildlife Ecology and Management, University of Freiburg, Tennenbacher Str. 4, 79106 Freiburg, Germany

[8] Department of Research and Documentation, Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany

* corresponding author

Keywords:
LiDAR; mixed step selection functions; multicategory response

Summary

Habitat selection can be considered as a hierarchical process in which animals satisfy their habitat requirements at different ecological scales. Theory predicts that spatial and temporal scales should co-vary in most ecological processes and that the most limiting factors should drive habitat selection at coarse ecological scales, but be less influential at finer scales. Using detailed location data on roe deer (*Capreolus capreolus*) inhabiting the Bavarian Forest National Park, Germany, we investigated habitat selection at several spatial and temporal scales. We tested (*i*) whether time-varying patterns were governed by factors reported as having the largest effects on fitness, (*ii*) whether the trade-off between forage and predation risks differed among spatial and temporal scales and (*iii*) if spatial and temporal scales are positively associated. We analysed the variation in habitat selection within the landscape and within home ranges at monthly intervals, with respect to land-cover type and proxys of food and cover over seasonal and diurnal temporal scales. The fine-scale temporal variation follows a nycthemeral cycle linked to diurnal variation in human disturbance. The large-scale variation matches seasonal plant phenology, suggesting food resources being a greater limiting factor than lynx predation risk. The trade-off between selection for food and cover was similar on seasonal and diurnal scale. Habitat selection at the different scales may be the consequence of the temporal variation and predictability of the limiting factors as much as its association with fitness. The landscape of fear might have less importance at the studied scale of habitat selection than generally accepted because of the predator hunting strategy. Finally, seasonal variation in habitat selection was similar at the large and small spatial scales, which may arise because of the marked philopatry of roe deer. The difference is supposed to be greater for wider ranging herbivores.

Introduction

Habitat selection can be considered as a hierarchical process in which animals constantly satisfy their habitat requirements at different ecological scales (Johnson, 1980; Hutto, 1985). Accordingly, past studies have investigated habitat selection at different spatial scales ranging from the selection of a plant species or food item (Gross et al., 1995; Shipley et al., 1998), of habitat patches (Coulon et al., 2008; Herfindal et al., 2009) and the habitat composition of their home range (Forester et al., 2007; McLoughlin et al., 2011), up to the geographical distribution of a species (Guisan and Zimmermann, 2000). Several studies have considered the different spatial scales of habitat selection, independently or simultaneously, showing that some ecological processes can be consistent across spatial scales or, conversely, different across scales (Boyce, 2006; Beyer et al., 2010; McGarigal et al., 2016). For instance, in moose (*Alces alces*), forage availability was associated with habitat use at the landscape scale but not at the within home range scale, where human disturbance and the availability of cover were more influential (Herfindal et al., 2009).

Although spatial and temporal scales often co-vary in ecological processes (Wiens, 1989), variation in habitat selection across temporal scales receives typically less attention than across spatial scales (but see Forester et al., 2007; Bjørneraas et al., 2011). Large herbivores show diurnal and seasonal patterns of activity that can potentially affect their habitat selection at different temporal scales (Owen-Smith et al., 2010). The most frequently considered temporal scale is seasonal variation in habitat selection (McLoughlin et al., 2011; Singh et al., 2012), probably as changes in environmental conditions are the largest between seasons. Migration has been found to be one strategy of ungulates to access high quality or abundant forage at all seasons (van Beest et al., 2010; Zweifel-Schielly et al., 2009; Cagnacci et al., 2011; Hebblewhite and Merrill, 2009). At a finer temporal scale, behavioural decisions are governed by short-term responses to immediate stimuli, such as the circadian rhythm (Ensing et al., 2014), rumination cycles in some herbivore species (Kamler et al., 2007), weather (Ewald et al., 2014b), olfactory cues (Eccard et al., 2015), or disturbance (Ciuti et al., 2012).

The decision rules, cues, and resources governing habitat selection by animals vary among different temporal scales (Orians and Wittenberger, 1991; Fortin et al., 2002). Habitat selection patterns should therefore vary at least as much between temporal scales as between spatial scales (Mayor et al., 2009). Assuming that behavioural decisions made at the largest ecological scales have the largest impact on fitness (Gaillard et al., 2010; Owen-Smith et al., 2010), Rettie and Messier (2000) suggested that the most limiting factors should drive habitat selection behaviour at coarse ecological scales, but be less

influential at finer scales. So far the empirical support for the limiting factor avoidance hypothesis across spatial scales of habitat selection is equivocal (support: Dussault et al., 2005; Hebblewhite and Merrill, 2009; Johnson et al., 2002) (no support: Aldridge and Boyce, 2008). While the limiting factor avoidance hypothesis (Rettie and Messier, 2000) has been originally formulated across spatial scales, it also predicts different patterns of habitat selection across temporal scales, whereby temporal variation in the most limiting factors should drive habitat selection patterns over coarse time scales. Obviously, no variation in habitat selection behaviour is to be expected in a constant environment (Doligez et al., 2003). However, if forage quantity varies seasonally more than predation risk, then selection for habitats offering food resources should show stronger seasonal variation than habitat selection against predation given that food is the most influential limiting factor. If predictable environments allow the avoidance of limiting factors at coarse temporal scales, then animals may take into account the limiting factors at fine temporal scales when selecting habitats in stochastic environmental conditions (Gaillard et al., 2010).

Habitats are selected for those properties such as food availability or cover that are related to the fitness of an individual (Clark, 1994). Among large herbivores, elk (*Cervus canadensis*) shelter from wolves (*Canis lupus*) in closed, forested habitats (Fortin et al., 2005); roe deer (*Capreolus capreolus*) strongly select ecotones where they can forage on highly digestible resources (Tufto et al., 1996); and moose seek habitats offering thermal cooling during the summertime (van Beest and Milner, 2013). Many ecological factors can modulate habitat selection by animals by changing the costs and benefits provided by the habitat (Lima and Dill, 1990). Animals may have to make behavioural trade-offs when different habitats confer opposing benefits, such as food quality or quantity vs. protection against predation (Brown, 1999; Godvik et al., 2009; Panzacchi et al., 2010). The magnitude and strength of the trade-off may vary in time as well as across time-scales, according to the relative influence of the different limiting factors.

In this study we took advantage of the fine temporal resolution of roe deer geolocation data in the Bavarian Forest National Park, and first describe the temporal variation in habitat selection with respect to land-cover type and continuous landscape variables, *i.e.* food and cover, in the context of predation by Eurasian lynx (*Lynx lynx*) and anthropogenic disturbance. According to McGarigal et al. (2016), this study is a multi-level analysis in both space and time and a multi-scale analysis in space. Using airborne Laser-scanning (LiDAR, Light detection and ranging, Ewald et al., 2014b), we assessed how food availability and fractional vegetation cover, estimated in summer, could account for the seasonal and diurnal variation in habitat selection by male and female roe deer.

Based on $n = 109,669$ geolocations on 52 roe deer (26 males, 26 females) monitored from 2006 to 2012, we tested the following predictions:

1) We expected that habitat selection would vary temporally on both a seasonal and the diurnal scale (Mysterud et al., 1999*a*, 1999*b*; Godvik et al., 2009). As large temporal scale processes should be strongly related to fitness (Mayor et al., 2009; Gaillard et al., 2010; Owen-Smith et al., 2010) we predicted that the seasonal variation in habitat selection would account for more of the temporal variability of habitat selection than diurnal variation. We further expected an interaction between both temporal scales as food availability and cover vary seasonally in temperate areas.

2) Applying the hypothesis of positive association between spatial and temporal scales (Wiens, 1989; Mayor et al., 2009) to different scales of habitat selection defined by Johnson (1980), we predicted that seasonal variation in habitat selection at the larger second order of selection (home range composition vs. landscape composition) should match the seasonal variation of habitat selection at the smaller third order of selection (composition of selected sites vs. home range composition).

3) We expected a stronger trade-off between food resources and shelter at the larger seasonal scale than on the smaller diurnal scale (Mysterud and Ims, 1998) as variations in habitat characteristics at the larger range of the temporal scale should be more constraining to the animal. First, according to the the limiting factor avoidance hypothesis (Rettie and Messier, 2000), if forage is the main limiting factor to roe deer, variation of habitat selection on a seasonal scale should be influenced by the availability of forage. Alternatively, if lynx predation is the primary limiting factor to roe deer, then variation of habitat selection on a seasonal scale should be strongly influenced by habitats offering the best protection against predation. Second, on a diurnal scale, we expected habitat selection to be associated with cover in response to human disturbance during the day (Herfindal et al., 2009; Bonnot et al., 2013). However, to reduce predation risk during the night, roe deer should seek more open areas to better spot predators (Panzacchi et al., 2010) or should more strongly select for human related habitats because lynx avoid the presence of humans (Basille et al., 2009).

Material and methods

Study area

The study area is located in the Bavarian Forest National Park (BFNP), which lies in south-eastern Germany along the border between the Czech Republic and Germany (cen-

ter coordinates: $49\,°3'19''N, 13\,°12'9''E$, Supplementary material Appendix 1, Fig. A1). The BFNP comprises a mixture of three major forest types structured along the elevation gradient. Above 1,100 m a.s.l. (16% of the area) are sub-alpine forests composed of Norway spruce (*Picea abies*) and mountain ash (*Sorbus aucuparia*). Hills between 600 m and 1,100 m a.s.l. are covered with mixed forests of Norway spruce, white fir (*Abies alba*), European beech (*Fagus sylvatica*) and sycamore maple (*Acer pseudoplatanus*) making up 68% of the area. In wet, cold valley bottoms (16% of the area), Norway spruce, mountain ash (*Sorbus aucuparia*) and birch (*Betula pubescens,* Heurich et al., 2010) dominate. Since the mid-1990s, the forests of the national park have been affected by a massive spruce bark beetle (*Ips typographus*) outbreak. By 2011, bark beetle attacks had resulted in the death of mature spruce stands over an area of about 6,000 ha (Lausch et al., 2013).

Roe deer are distributed over the whole of the BFNP, occupying a 24,218 ha area. Management of roe deer in the BFPN is limited to the wild ungulate management zone ($\approx$ 29% of the study area), which prohibits hunting in a core area of 17,000 ha (Möst et al., 2015). The estimated roe deer population density was low during the study period, ranging from 1–3 animals km^{-2}. Red deer also occur in the BFNP at an estimated density of 1.56 animals km^{-2}. During our study, roe deer in the BFNP were subject to predation by European lynx which had been reintroduced in the 1980s (Wölfl et al., 2001). Between 2005 and 2012, of the 168 individuals monitored 30% were killed by lynx, making up about 50% of the mortality recorded. An additional 7% were killed in road accidents (Heurich et al., 2012*b*). At present, the lynx population is stable in the BFNP (Müller et al., 2014), with an estimated density of between 0.4 to 0.9 lynx 100 km^{-2} in the core area (Weingarth et al., 2012).

Roe deer geolocation data

We used wooden box traps to capture roe deer during the winter months (from October to March) baited with pomace, maize or silage. Traps were set during the evening and inspected the following morning. We handled the deer and attached GPS-collars without using chemical tranquilisers (Weilnböck et al., 2012). GPS-GSM collars (series 3.000) from VECTRONIC Aerospace, Berlin (Germany) were used to record roe deer locations using a variety of sampling regimes, ranging from every 3 min to every 12 h. We removed the first 10 days of each survey period to exclude any effect of the capture and handling process on the animals' behaviour (Morellet et al., 2009). For the analysis we excluded those animals whose fix success rate, defined as the number of successfully

stored locations divided by the number of attempts (Frair et al., 2010), was below 90 percent.

We used a total of 172,507 fixes from 52 roe deer (26 males, 26 females) before thinning ranging from 136 to 17,044 fixes per individual (mean: 3,317, sd: 2,897) over a period from 14 to 2,081 days (mean: 484, sd: 397). The spatial accuracy of the fixes was 10 m on average with a maximum recorded error of 16.3 m (Stache et al., 2012).

Habitat characterisation and resource classification

We used spectrozonal aerial images of the study area from 2008 (Heurich et al., 2012*a*) to classify forest areas according to land-cover type (Belyaev et al., 2004). We classified land cover into 11 habitat classes (Table I.1). We refer to the Supplementary Material Appendix 1 for a description of seasonal variation in the availability of forage and cover in the different habitat types. We estimated vegetation cover from airborne LiDAR data acquired using a Riegl 680i laser scanner (350 KHz, nominal point density 30-40 points m^{-2} ; altitude 650 m recorded at a 0.32 m footprint). Under leaf-on conditions data were acquired within three days in June 2012 from the entire national park area. LiDAR measurement points were grouped into a 5×5 m grids and for each grid cell, we calculated inverse penetration ratios at a height of 2-60 m above ground. This penetration ratio is an estimation of the fractional vegetation cover at this height (see Ewald et al., 2014b; Latifi et al., 2015, for more information). As we do not have a direct measure of predation risk we use this cover variable as a proxy for predation risk. Cover was found to be positively related to predation risk in other studies on lynx and roe deer (Podgorski et al., 2008; Lone et al., 2014). From a roe deer perspective, the greater the cover index, the higher is the predation risk. Lynx are solitary, stalking predators, and rely on remaining undetected until they come within about 20 m of their prey to initiate an attack. Attacks from larger distances are usually unsuccessful (Haglund, 1966).

We assessed the relative food quantity for each habitat type based on estimations of herbaceous biomass using a vegetation model PhytoCalc (Heinrichs et al., 2010). PhytoCalc relates plant species biomass to its cover and shoot length values using species-specific allometric equations. We measured cover and shoot length values from vegetation surveys conducted in June, July and August in 2009 to 2011 on 282 plots scattered over the national park. The sampling design and coverage estimation method are described in Ewald et al. (2014a). Shoot lengths of 20 individuals were measured for all species with coverage exceeding 1%. Because the PhytoCalc estimation is restricted to forest ground vegetation, the biomass of the herbaceous layer from cultivated and unmanaged

meadows was derived empirically by harvesting (4×1 m^2), drying (60 °C, 2 days) and weighing samples from 31 plots. The R^2 of the linear regression between values estimated by PhytoCalc and real biomass values is between 0.52 and 0.57 (Ewald et al., 2014a). Because we had more than one value for each land-cover type, we chose the median value to define the relative food quantity of each habitat (Table I.1). As a concentrate feeder, food selection of roe deer should be driven more by the availability of high quality forage rather than by the overall biomass (Lashley et al., 2015). However, total herbaceous biomass being related to food quality (Saïd et al., 2005), we used biomass as an overall proxy for the availability of forage plants that roe deer seek after.

Statistical analysis

We analysed the temporal variation in habitat selection of roe deer using three complementary approaches: i) by comparing the monthly home range composition of individual roe deer to the available habitat at the landscape scale, ii) selection of habitat types within monthly home ranges; and iii) selection of the resources cover and biomass. The first and second analysis of habitat type selection provides information on temporal variation in the selection of habitat categories on the second and third order of Johnson's (1980) scale. We set out to illustrate that sites sharing the same environmental factors (pooled as habitat types) are visited with varying frequencies throughout the day and throughout the year. With the third analysis we tried to understand these time-related patterns of habitat selection by considering the fine-scale spatial heterogeneity of the landscape using continuous variables.

Modelling habitat selection

Resource selection functions (RSF, Manly et al., 2002) using logistic regression models to estimate parameters of interest have been the most popular tool used to link spatial patterns of animal locations to landscape characteristics (Duchesne et al., 2010; McLoughlin et al., 2010). If each resource unit is classified into one of several categories, such as habitat type, then habitat selection can be measured using selection ratios (SRs) that are comparable between categories (ch. 4, Manly et al., 2002). The SR of a category is proportional to its selection probability, on condition that the animal has access to all available units of the habitat. We investigated the time variation in habitat selection of roe deer at two spatial scales by modelling time-dependent SRs of 11 habitats using multicategorical models. To ensure that there are no auto-correlations between successive steps, we investigated variograms (Fleming et al., 2014, details in the Supplementary

material Appendix 2). We used the time interval where the variogram reached 90% of the home range size as the minimum time interval between successive steps in the analysis of monthly habitat selection (Fleming et al., 2014). In our data this interval was approximately 25 h. We included only those individuals with more than 70 recordings. Our data set contained then n =15,267 locations of 17 females and 19 males.

Second order spatial scale

We compared habitat availability a_i and use u_i of habitats $i = 1, ..., 11$ (Tab. 1) on the landscape scale by computing monthly SR as $w_i = \frac{u_i}{a_i}$ (McLoughlin et al., 2007). Habitat availability at the landscape scale was defined as the proportion of the different habitat types in the area covered by the 90% utilization distribution kernel of all locations of all roe deer (red bordered polygons in the supplementary material in Fig. A1). Habitat use for a given deer was defined as the proportion of a habitat in its monthly 95% minimum convex polygon home range for each individual and month (coloured polygons in the supplementary material in Fig. A1). For details about the model selection process see the supplementary material A3.

Third order spatial scale

Multicategorical logit models can be fitted using baseline-category logit models (Agresti, 2002). We set the habitat type with the highest prevalence as the baseline, which in our case was the old mixed stand habitat type, found in 27% of all recorded locations. Given the multinomial structure of the model, it provides for the probability of choosing the baseline category K: $\pi_K(x_j) = 1 - \pi_1(x_j) - \ldots - \pi_{K-1}(x_j)$. Probabilities $\pi_i(x_j)$, $i = 1, \ldots, K-1$ were estimated by fitting $K-1$ binary logit models. The ith model included observations from habitat i and K only, where $y_j = 1$ if an individual j was observed in habitat i, and $y_j = 0$ if it was observed in the reference habitat K. The probability of occurrence was estimated via the logit link.

We accounted for the variation in availability of habitats among individuals and over time as follows. First, we calculated the monthly 100% home range (minimum convex polygon) for each individual. Home ranges of individuals presenting a biologically unrealistic size due to dispersal were discarded, using the 90% percentile as a cut-off value (for females: 182 ha, males: 459 ha). Second, we used a rasterized landscape with grid cell size of $10 \times 10m^2$ to obtain the relative availability of each habitat type within the monthly home ranges. Last, we calculated the relative availability a^r of habitat type i, i.e. the fraction of the area covered by habitat type i, in the home range of each different

animal j and for each time of the year (m, month). We accounted for the variation in habitat availability in our multicategorical logit models by entering the logarithm of the availability $a_{jm}^{(i)}$ of a land-cover type within the corresponding monthly home range of the animal j as an offset term (called "base rate" in Manly et al. (2002, ch. 7)). Animals were discarded from the analysis of a habitat if the habitat was not available in the home range.

Variation in selection across individuals and years were accounted for by including random effects on the intercept for individuals (Gillies et al., 2006) and years. Variation in habitat selection on the daily and seasonal scales was tested by including a term for either time of day (hour) or time of year (month), modelled by a cyclic smooth function (Wood, 2006). We tested for the interaction of both temporal scales by including a tensor product smooth function over time of day and time of year. Smooth functions were calculated either with or without distinguishing between the sexes. The model selection process was based on AUC and is described in the Supplementary material Appendix 4.

Modelling resource selection

We used SSF to test whether the habitat properties of food and cover influence habitat selection of roe deer. The actual locations chosen were compared stepwise with locations that might have been chosen out of the direct surroundings of the last step. This allows inferences regarding habitat selection on finer temporal and spatial scales (Thurfjell et al., 2014). To ensure that there are no auto-correlations between successive steps, variograms (Fleming et al., 2014) suggested using a time interval of at least four hours between two successive steps for all individuals (see Supplementary material Appendix 2 for more information). We included only those individuals with more than 70 recordings. This data set consisted of 63,490 locations of 17 females and 20 males. According to the SSF framework, 10 random locations were sampled for each location based on parametric distributions for turning angle (uniform) and step lengths (exponential with parameter λ equals twice the sample mean of observed step lengths, here: for females 241.6 m, for males 355.2 m; see Supplementary material Appendix 9 for a comparison of three different sampling designs in the SSF framework, Forester et al., 2009). Separate models were fitted for diurnal and seasonal scales, respectively for each season: Winter (December–March), Summer (May–Sep), Spring/Autumn (Apr, Oct, Nov) and time of day by photoperiod: night, day, twilight where the time of twilight was defined as the time between first light and sunrise or sunset to last light (nautical twilight), respectively.

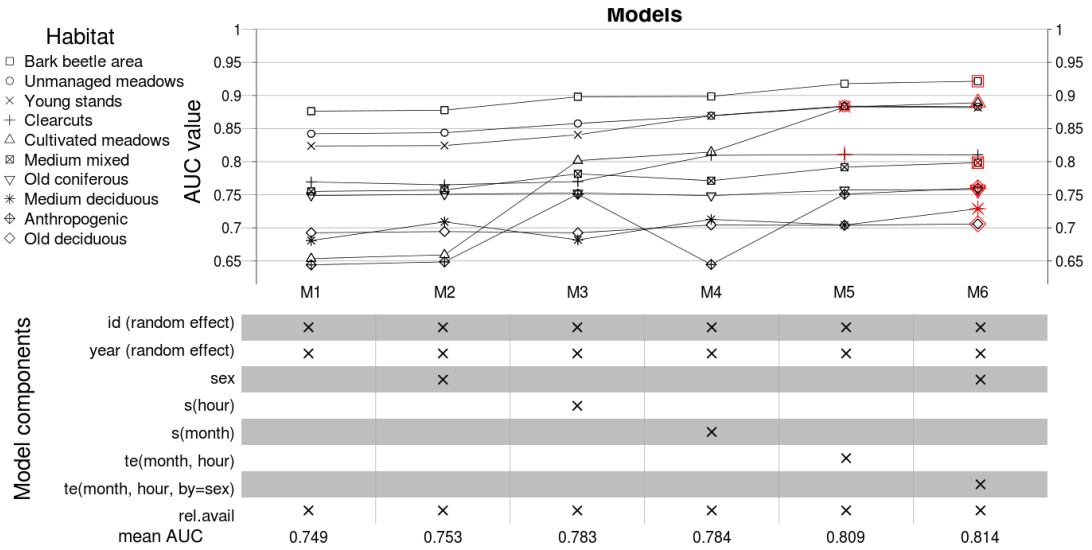


Fig. I.1 AUC values for models explaining the selection of 11 habitat types by 52 roe deer (26 males, 26 females) in the Bavarian Forest National Park, Germany from 2002 to 2011. AUC-values are in ascending order of the sum of AUC-values (over habitats). The greater the AUC value, the better the predictive accuracy of the model. Model components integrated in the model are shown in the table at the bottom of the figure. All models included the variable id (for individual) and year as random effects. The red symbol indicates the model with the highest AUC-value for a habitat. Abbrevations: rel.avail, relative availability of habitat type; s, smooth term, for hour and month (it is a cyclic smooth function); te, cyclic tensor product smooth term; by, a replicate of the smooth term, it is produced for each factor level of each sex.

We estimated the parameters of the SSF with mixed conditional logistic regression models using the package *TwoStepClogit* (Craiu et al., 2012). We tested for variation in the coefficients over time of day and time of year by including B-spline smoothing functions (Wood, 2003). The number of basis functions (rank) for time over year and time over day refers to the flexibility of the curve. The maximum number of the rank was six because a higher rank would have demanded a higher resolution of GPS fixes in time for all individuals. The model selection process is described in the Supplementary material Appendix 5.

We performed all analyses in the statistical software **R** (R Core Team, 2015) using the packages *mgcv* (Wood, 2006) for GAMMs, *adehabitatLT* for home range calculations (Calenge, 2006), *Hab* package (Basille, 2014) for random point generation and *maptools* (Bivand and Lewin-Koh, 2013) for determining the time of day relative to sunrise and sunset.

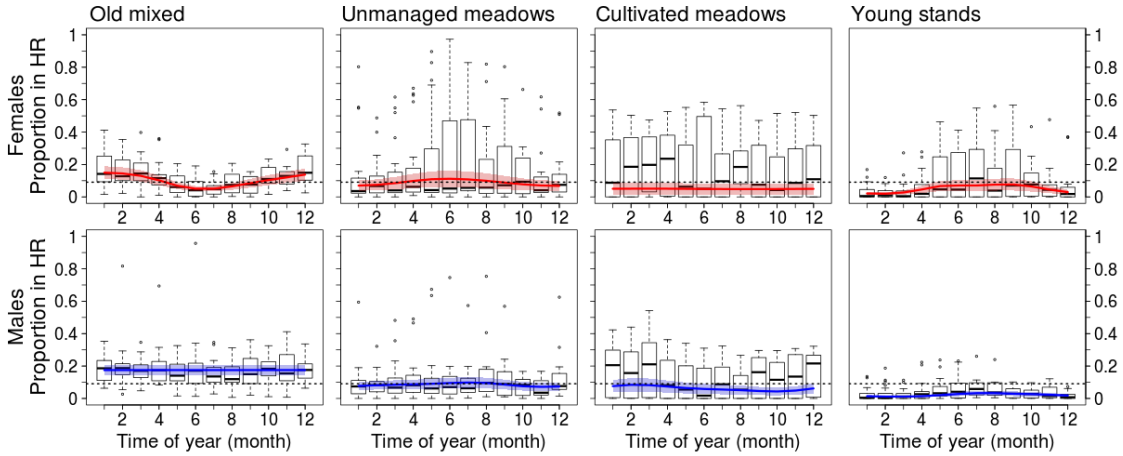


Fig. I.2 Habitat selection on 2nd order (landscape scale): Estimated selection ratios from generalized additive mixed model for 17 female (top panel) and 19 male (bottom) roe deer in the Bavarian Forest National Park, Germany recorded from 2002 to 2011; shaded areas indicate 95% pointwise confidence intervals. Boxplots show variation of the proportions of habitats in the home ranges over the time of year.

Results

Seasonal Second Order Habitat Selection (Landscape Scale)

The mean monthly home range size was 70.4 ha (sd: 41.5 ha) for females and 152.8 ha (sd: 101.7 ha) for males. Habitat composition within monthly home ranges differed markedly from that of the study area for most of the eleven habitat types (Supplementary material Appendix 3, Figs. A2, A3). We found a significant seasonal variation in the selection ratios for almost all of the habitat types with the exception of cultivated meadows for females and old mixed stands for males, with different patterns for males and females (Figs. I.2, A2, A3).

While males highly selected old mixed stands constantly throughout the year, females showing in general a higher selection in winter and a lower selection in summer (Fig. I.2). Selection of young stands and unmanaged meadows were higher in summer than in winter, for both males and females. Higher selection in summer than in winter was also found for medium mixed, bark beetle area, medium and old deciduous stands. A higher selection in winter was found for medium deciduous, anthropogenic area, clearcuts (only for females), cultivated meadows, and all old stands.

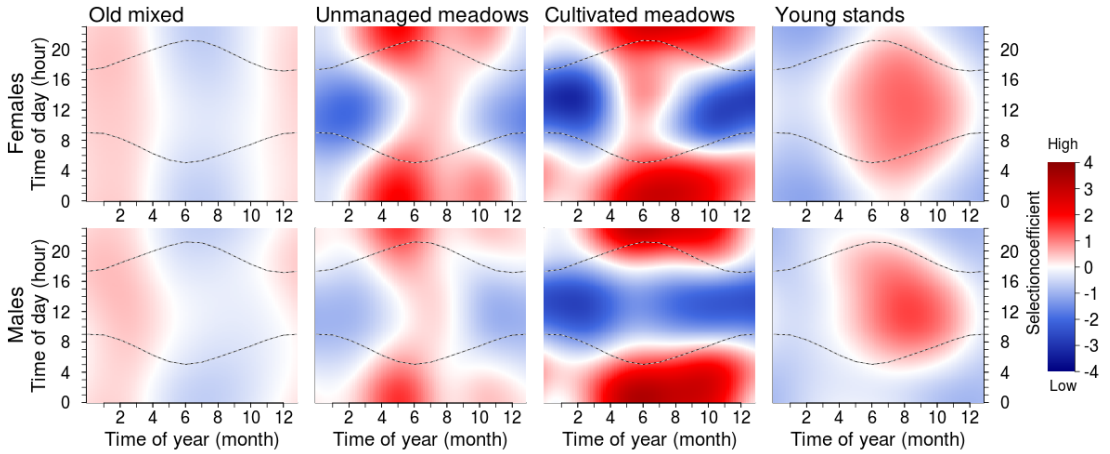


Fig. I.3 Habitat selection on 3rd order (within home range): Variation of the selection coefficient over time of year (x-axis) and day (y-axis) for 17 female (top panel) and 19 male (bottom) roe deer in the Bavarian Forest National Park, Germany recorded from 2002 to 2011. Horizontal lines show the times of sunrise and sunset.

Third Order Habitat Selection - Interaction between the Seasonal and Diurnal Scales

Habitat selection by roe deer of both sexes showed marked time-variation for all habitat types, and diurnal and seasonal temporal scales interacted with each other (Fig. I.3, Supplementary material Appendix 7, Figs. A4, A5). The main pattern was that habitat selection varied more strongly at the seasonal scale, and models that included seasonal variation had a higher predictive accuracy than those without, for almost all habitats except from anthropogenic area and medium mixed (e.g., AUC=0.77 for clearcuts with variation over day; AUC=0.82 with variation over year). When variation over both temporal scales was considered, the predictive accuracy increased to a mean of 0.809 (M5, Fig.I.1, min: 0.7 for old deciduous, max: 0.92 for bark beetle area). Including sex as a predictor increased the predictive accuracy for all habitats (M6, mean: 0.814) but young stands, unmanaged meadows and clearcuts.

Overall, the diurnal pattern in habitat selection was consistent throughout the year for most habitat types (e.g., cultivated meadows: highly selected during the night and rarely selected during the day), the magnitude of the selection simply varying by the time of year (e.g., cultivated meadows: high in summer and low in winter). The variation in the magnitude of selection over the course of the year resulted in a seasonal alternation between high and low selection of most habitats (Fig. I.3) The interaction between diurnal and seasonal variations of habitat selection is clearly driven by variations in day

length (Fig. I.3).

The observed temporal variation in selection coefficients was the largest for habitat types closely associated to food resources such as meadows and anthropogenic area. For cultivated meadows for instance, selection coefficient showed the largest variation at the diurnal (sd: 1.4) and seasonal scale (sd: 0.8) in comparison to bark beetle areas (sd over diurnal scale: 0.7 vs. sd over seasonal scale: 0.56), medium aged mixed stands (0.4 vs. 0.16) or anthropogenic (0.8 vs. 0.005). Other habitat types showed a higher variation over the seasonal scale than over the diurnal scale: unmanaged meadows (sd over diurnal scale: 0.36 vs. sd over old deciduous (0.0001 vs. 0.23), old coniferous (0.08 vs. 0.14) and medium aged deciduous (0.00008 vs. 0.11).

Seasonal Variation of Second and Third Order Habitat Selection

As expected from the hypothesis of positive association between spatial and temporal scales (Wiens, 1989; Mayor et al., 2009) we found a strong positive relation between the seasonal patterns of the selection on second order and third order scales for most habitats (eight of eleven, Tab. I.2). In regards the comparison between the two spatial scales we calculated the correlation of the SR over the seasonal scale. For the smaller third order scale we averaged the values over the diurnal scale to correlate the mean selection values per month with the monthly SR of the second order scale. This was done for males and females separately. For most habitats the correlation was very high (Tab. I.2) for both sexes. Exceptions are found for cultivated meadows and medium deciduous stands. Only for males, was the positive correlation for old deciduous and coniferous stands and medium aged stands not significant.

Trade-off between Food Resources and Cover

Variation in selection for cover and biomass varied markedly diurnally and seasonally (Fig. I.4). At both temporal scales, time-variation in resource selection improved the model prediction compared to a model with a constant resource selection over time (Tabs. I.3, I.4) except for winter. For male roe deer in all cases the interaction between fractional cover and biomass explained the highest degree of variation in site selection. However, for females including biomass as a predictor did not improve model prediction and only in winter did biomass influence site selection by females without any detectable temporal variation over time of day.

We expected a trade-off between forage and shelter and, indeed, detected a negative

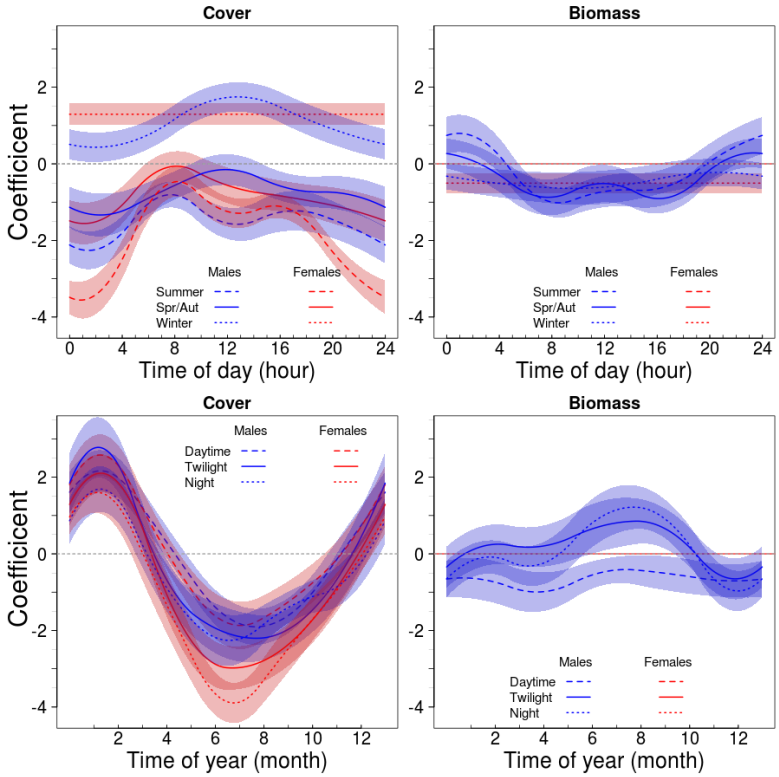


Fig. I.4 Variation in the selection coefficient for cover (left) and biomass (right) over time of day (top panel) and year (bottom panel) for 26 male (blue lines) and 26 female (red lines) roe deer recorded from 2002 to 2011 in the Bavarian Forest National Park, Germany over summer time (dashed line), spring/autumn (solid) and winter (dotted), respectively, during the daytime (dashed line), twilight (solid) and nighttime (dotted), based on step selection functions. Shaded areas indicate the 95% pointwise confidence limits.

relationship in time between selection for cover and for biomass on both, seasonal and diurnal scales. The temporal correlation between selection for cover and biomass was moderately negative at the seasonal scale (-0.58, -0.57 and -0.67 for day, twilight and night respectively). At the diurnal scale, correlation coefficients were highly negative in summer (-0.88), moderately high in spring/autumn (-0.6) and low for winter (-0.43). In contrast, the landscape fractional cover and biomass were moderately negatively correlated ($r = -0.58$).

Cover accounted for slightly more variation in resource selection by roe deer at both temporal scales (maximum predictive accuracy on the seasonal scale $R^2 = 7.2$ %, on the diurnal scale: $R^2 = 8.8\%$) than did biomass (maximum on the seasonal scale $R^2 = 6.9\%$, and on the diurnal scale: $R^2 = 6.98\%$). The explained variance in site selection due to cover and food varied between seasons and the day but was relatively low. At the

seasonal scale the highest predictive accuracy was found for night (males: 7.5, females: 6.6) and lowest for day (males: 3.5, females: 4.4). On the diurnal scale highest predictive accuracy was obtained in summer for females (8.8). For males summer was the season with the lowest R^2 (3.8); highest were found in winter (6.6), when models for females obtained the lowest predictive accuracy (3.5).

Roe deer showed a high selection of open sites during the nightime (selection coefficient (SC) for cover in summer at night: for males -2.24 (±0.49 (SE)), for females -3.87 (±0.52). During the day cover seemed to influence site selection to a lower extent, as SC are closer to 0, in particular in spring/autumn. For summer the SC is closer to 0 during dawn (e.g., for males -0.81 (±0.33)) than during noon (-1.89 (±0.46)) and dusk (-1.45 (±0.48)). In winter habitats providing cover were more strongly selected by females throughout the day (SC= 1.29 (±0.28)). For males the selection of cover was even higher during day (SC= 1.74 (±0.38)) than during night (SC= 0.51 (±0.39)). Only male roe deer showed a higher selection of biomass rich sites during summer (SC at night 1.14 (±0.61)) and twilight 0.81 (±0.64)) and a higher selection of low forage sites during winter for all times of day (SC: -0.73 (±0.55)). During day male roe deer selected sites with low biomass (almost constant SC: -0.68 (±0.42)).

Discussion

As a prey species, we expected roe deer behaviour to be largely responsive to predation, but with regards to habitat selection, we found support of a rather predominant role of forage availability over lynx predation risk. First, the large-scale temporal variation in habitat selection by roe deer seems primarily governed by food resources, and to a much lower extent by predator avoidance or human disturbance. Second, the trade-off between selection of habitat for forage and protection against predation is weak, and of similar magnitude than the one observed at the landscape level. Hence, the landscape of fear might not systematically apply to all predator-prey systems, depending for instance on the predator's hunting tactic and density.

Forage, the Main Driver of Habitat Selection

Because of its direct effect on mortality and the indirect induced sub-optimal use of habitats, predation is generally regarded as the main factor limiting the fitness of large herbivores (Lima and Dill, 1990). Rettie and Messier (2000) argued that limiting factors greatly affecting the species' fitness should be avoided at coarser spatial and temporal

scale. Consequently, we expected roe deer to avoid predation by lynx by selecting habitats offering the most effective shelter at coarse temporal scales (Rettie and Messier, 2000). Seasonal habitat selection pattern by roe deer however matches with temporal variation in food resources over time at both spatial scales of habitat selection (Figs. I.2, I.3). For instance, undergrowth in young stands provides cover and optimal foraging for roe deer with, *e.g.* mountain ash and herbaceous vegetation, and is selected in summer. In contrast, the risk of predation by lynx being on average lower in winter than in summer in the BFNP (Belotti et al., 2013), one could expect roe deer to select habitat offering shelter against predation in summer. We report the opposite pattern. Roe deer highly selected habitats with a high risk of predation (*e.g.* unmanaged meadows, clearcuts, Tab. I.1) at both the second and third scale of selection (Johnson, 1980). Finally, during winter sites providing cover were sought after when woody plants also form an important food resource for roe deer at a time when availability of herbaceous plants is low because of snow cover (Barančeková et al., 2010). Moreover, the presence of artificial feeding sites could drive roe deer in forested areas at BFNP in winter, in addition to thermal shelter and reduced movement costs linked to thick snow layer (Ewald et al., 2014b). Consequently, at every time of the year roe deer strongly selected habitats based on forage availability. Overall, these results suggest that food, and not predation, is the main limiting factor for roe deer in the BFNP.

That forage availability drives most of the seasonal variation in habitat selection behaviour by roe deer agrees with the specific energy allocation tactic of this species. Roe deer are concentrate feeders preferring energy-rich foods (Tixier and Duncan, 1996), with a rapid process of digestion (Hofmann, 1989) requiring frequent and regular food intakes, which cannot be delayed for extended periods of time. In addition, female roe deer being income breeders (Jönsson, 1997) the availability of food resources at the time of parturition is the main driver of their reproductive success (Andersen et al., 2000; Pettorelli et al., 2005). Males are also actively engaged in an energy demanding territory defense from April to September, with an activity peak in August (Johannsson, 1996; Melis et al., 2005). Tracking vegetation flush in spring and selecting habitats offering highly digestible food is therefore of prime importance to roe deer of both sexes, and failing to do so would likely lead to a reduction in reproductive success. Contrary, because of their ability to use stored energy to raise their young, species like red deer or caribou (*Rangifer tarandus*) with a capital breeding tactic of resource allocation to reproduction may be less risk prone in terms of habitat selection than income breeders during breeding. Consequently, capital breeders may show a stronger avoidance of predation than income breeders (e.g. Hebblewhite and Merrill, 2009, on elk).

The overwhelming importance of forage over predation for roe deer is also reflected by the trade-off between selection for forage and cover. Previous works on roe deer suggested that habitats are selected either for maximizing food intake (Mysterud et al., 1999*b*; Pellerin et al., 2010) or for reducing predation risk (Linnell et al., 2004; Bongi et al., 2008; Panzacchi et al., 2010). In BFNP, the temporal variation in selection coefficients for cover and for forage are apparently negatively correlated and similar at both temporal scales for males (Fig. I.4). By selecting habitats for forage in summer, male roe deer also avoid densely covered habitats and may find themselves at lower risk of predation because lynx hunt for their prey in covered areas with low visibility (Podgorski et al., 2008; Valeix et al., 2009; Lone et al., 2014). For females, no significant relationship between selection for food and cover did occur that we interpreted as resulting from a more risk adverse habitat selection behaviour than for males because females use safer habitats close to human settlements, as regularly reported among large herbivores with highly vulnerable offspring to predation (Main and Coblentz, 1996). Although the trade-off between foraging and protection from predators is supposed to be inherent to habitat selection by prey species such as large herbivores (Houston et al., 1993; Brown and Kotler, 2004; Hebblewhite and Merrill, 2009; Mabille et al., 2012), the apparent negative association between selection for food and cover we found for roe deer could simply result from the habitat structure rather than from a behavioural trade-off. In fact, the temporal correlation between selection coefficients for forage and for cover is of similar magnitude than the correlation between the two variables in the landscape in the BFNP, where locations providing abundant food resources also have generally lower cover values ($r = -0.56$). However, because we did not account for seasonal variation in forage and cover supply the negative association was probably less pronounced in winter.

Predictability and Variability of Environmental Factors

Prey species are assumed to live in a landscape of fear in which animals permanently adjust their spatial behaviour to the perceived predation risk (Laundré et al., 2010). However, empirical evidence suggests that this response is hierarchical and context-dependent (Hebblewhite et al., 2005), and not systematically observed at large spatio-temporal scales of habitat selection. For instance, caribou (*Rangifer tarandus*) living under wolf (*Canis lupus*) predation in Western America select habitats at large spatial scales more in relation to food than to predation risk (Avgar et al., 2015). Similarly elk in the Yellowstone NP did not show wolves avoidance in winter (Mao et al., 2005) and were suggested to rely on alternative anti-predator strategies such as higher vigilance. Roe

deer in the BFNP also showed small scales behavioural responses by increasing vigilance when confronted with pulses of high predation risk (Eccard et al., 2015). At large spatial and temporal scales roe deer select habitats providing high quality forage over those decreasing predation risk (see Samelius et al., 2013). Predation represents the highest cause of mortality in roe deer of the BFNP (Heurich et al., 2012*b*), but depending on the environmental context, especially the predator's hunting strategy and density, predation might not be perceived by large herbivores as the most limiting factor. Lynx are solitary stalking and ambushing predators (Belotti et al., 2013). From a prey point of view, lynx attacks are difficult to predict in time and space. Lynx is an elusive and highly efficient predator whereby 70% of lynx attacks are successful (Haglund, 1966). In comparison, in only 5-22% of wolf attacks the roe deer were killed (Wikenros et al., 2009). In combination with the low lynx density (Weingarth et al., 2012), the highly efficient predation by lynx might leave few opportunities for its prey to learn where the riskiest areas are located. In comparison, in a predator-prey system in Montana, USA, where mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) are preyed by wolves and cougars (*Puma concolor*), both prey species selected their habitat (3rd order) to limit enccounters with wolves, a typical coursing predator (Atwood et al., 2007). However, habitats with high risk of predation by cougar as an ambush predator where highly visited by mule deer. Elks even shifted towards those risky habitats to avoid wolf predation. In a predator-prey system involving a single cryptic predator such as lynx or cougar, prey may show limited large-scale anti-predator habitat selection. More generally, predation is likely an immediate stimuli for large herbivores, that occurs on an encounter-by-encounter basis, generating rather small spatio-temporal scales behavioural response (Creel and Winnie, 2005; van Beest and Milner, 2013; Basille et al., 2015). Alternatively, given the high selectivity of roe deer diet, the indirect long-term fitness costs of predation induced by the use of sub-optimal habitats might outweigh its direct costs because of its low probability of occurrence (Creel and Christianson, 2009).

Following Rettie and Messier's (2000) hypothesis, our results could suggest that human disturbance is a more limiting factor to roe deer than predation in the BFNP. During the day, roe deer indeed select habitat types that provide cover. Hiding behaviour usually occurs in places frequently visited by humans, and in open areas where they can be disturbed, and roe deer seek refuge in closed habitats during the day (Fig. I.4, Herbold, 1995). The use of human related habitats (settlements, roads, cultivated meadows) by roe deer varies more strongly over time of day than over seasons in the BFNP (Fig. I.2, Supplementary material Appendix 7, Figs. A4-A7) likely to avoid encounters with humans (Benhaiem et al., 2008; Shannon et al., 2014) despite hunting only occurs in

autumn and winter and despite most roe deer are not hunted within the BFNP. Habitat selection at the different scales of selection may hence be the consequence of the temporal variation and predictability of the limiting factors for an individual as much as it is associated with fitness (Rettie and Messier, 2000). For instance, in the BFNP human disturbance is certainly more predictable than is predation by lynx, and hence a better predictor for habitat use of roe deer. Similarly, in the BFNP forage quantity varied seasonally more than predation risk, and roe deer habitat selection showed stronger seasonal than diurnal variation (Fig. I.4). Accounting for the spatio-temporal variability of limiting factors in the framework of Rettie and Messier's (2000) hypothesis might help at understanding why this hypothesis is only partially supported so far.

Convergence of Processes at Large Spatial and Temporal Scales

In most ecological processes, a positive association is expected between spatial and temporal scales (Wiens, 1989; Mayor et al., 2009) because seasonal phenomenons like plant phenology should have stronger effects on the larger scales of habitat selection than on the fine-scale ones. Movement ability of the animals should drive the association between spatial and temporal scales of habitat selection (Mayor et al., 2009). Although partial migration is reported in some areas, roe deer is mostly philopatric and has restricted movements for a medium-sized mammal (Cagnacci et al., 2016). Home range should hence stay on the same location and should have little changes in composition in time. At the BFNP, we nevertheless found that the small monthly variation in home range composition of roe deer leads to a marked seasonal pattern at the 2nd order of habitat selection (Fig. I.2), similar to wider-ranging species like wapiti or caribou (Boyce et al., 2003; Rettie and Messier, 2000). In addition, the seasonal variation in habitat selection was strongly and positively correlated at the 2nd and 3rd order scales, but for cultivated meadows and medium deciduous forests (Table I.2). Given the restricted ranging behaviour of roe deer, large scale movements are small and may confound with movements at smaller spatio-temporal scales. For resident roe deer, we might describe the same behavioural decision rules in space use for home range relocation and for habitat patch choices. At the seasonal time scale, roe deer seem to choose home range composition and feeding sites in response to the same environmental drivers for most habitat types. In summer for instance, young stands provides both cover and high quality forage to roe deer and makes a larger proportion of both the surface area of the home range and time spent in the different habitats than during winter (Figs. I.2 and I.3). The choice of using young stands is therefore governed by broad-scale decisions in response to the relatively

slow variation in food resources availability over the year. Conversely, the selection of cultivated meadows is strongly diurnal in response to short-term variation in risk of human disturbance risks, which completely breaks its connection with the seasonal-scale decisions (Table I.2). The relationship between long temporal and broad-spatial scales likely depends of habitat types and associated resources selected by animals. Our study suggests that this association could be species-specific and determined by its ranging behaviour and ability. We therefore predict much more pronounced differences in habitat selection patterns between temporal and spatial scales or between 2nd and 3rd order scales of habitat selection for species like elk or caribou with larger movements and a much less restricted annual home range than roe deer.

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Tab. I.1 Overview of availability of habitat types in the study area and availability within the home ranges; the latter is the median for all individuals in order of decreasing selection. The values for cover are the means (and standard deviations) of the fractional cover above 2 m over the study area derived from high resolution airborne Laser-scanning (LiDAR, Light detection and ranging) in summer. Biomass is the average value of dried biomass within 1 m^3 of a habitat type. Predation risk is based on a preliminary study, with ++ being very high risk, + high risk, 0 medium risk, and − low risk.

Habitat	Avail. in study area	Avail. in home ranges	Cover	Biomass (gm^{-3})	Predation risk
Young stands	0.0203	0.0084	0.36 (0.27)	54 (-)	+
Unmanaged meadows	0.0203	0.0154	0.31 (0.26)	349 (41)	++
Medium aged deciduous	0.0146	0.0057	0.66 (0.36)	89 (114)	0
Clearcuts	0.0459	0.0263	0.25 (0.24)	29 (57)	++
Bark beetle area	0.1108	0.0041	0.31 (0.24)	10 (53)	+
Medium aged mixed	0.0747	0.0467	0.67 (0.33)	85 (80)	+
Cultivated meadows	0.0511	0.0701	0.16 (0.2)	299 (91)	−
Old deciduous	0.1838	0.2065	0.77 (0.31)	45 (79)	−
Old coniferous	0.2204	0.204	0.63 (0.35)	24 (58)	−
Anthropogenic	0.0273	0.0237	0.36 (0.33)	300 (-)	−−
Old mixed	0.2309	0.3891	0.73 (0.34)	54 (75)	−

Tab. I.2 Correlation between the variation of 2nd and variation of 3rd order selection of habitats over the seasonal scale. 3rd order selection was averaged over time of day; which is the mean within home range selection per month.

	females	males
Bark beetle area	0.894	0.831
Unmanaged meadows	0.811	0.855
Cultivated meadows	-0.800	-0.880
Clearcuts	-0.355	0.428
Young stands	0.930	0.956
Old mixed	0.891	0.856
Old deciduous	0.923	-0.084
Medium mixed	0.883	-0.782
Medium deciduous	-0.313	-0.365
Anthropogenic	0.749	0.691
Old coniferous	0.611	-0.353

Tab. I.3 Mean R^2 (in percent) for models explaining the effect of cover and biomass on variation in site selection (deviation from random choice) over **time of day**. The higher the R^2, the more accurate the prediction of a new data set (using 5-fold cross-validation). nk refers to the number of basis functions used to build the spline, which equals the number of parameters estimated for each variable. For each season (summer, spring/autumn, winter) three models were estimated, including either cover, biomass, or both as explanatory variables for site selection. Different flexibilities (nk) of the spline modelled the variation in the coefficient over time of day. In the linear case there was no variation and a constant selection of cover or biomass over years was assumed, respectively . Null deviation is based on a model where each proposed location in one step was assigned the same probability. Bold values refer to the highest value of R^2.

Sex	Season	Variables	const	nk=3	nk=4	nk=5	nk=6
males	Summer	cover+biomass	2.87	2.91	3.51	3.63	**3.78**
		cover	3.05	2.97	3.31	3.35	3.51
		biomass	1.99	2.07	2.65	2.79	2.92
	Spr/Aut	cover+biomass	3.65	3.73	3.93	4.00	**4.06**
		cover	3.71	3.76	3.93	3.98	3.98
		biomass	3.46	3.49	3.66	3.75	3.81
	Winter	cover+biomass	6.56	6.53	**6.61**	6.58	6.60
		cover	6.46	6.46	6.51	6.48	6.50
		biomass	6.21	6.20	6.22	6.20	6.22
females	Summer	cover+biomass	7.70	7.84	8.39	8.46	8.54
		cover	8.29	8.26	8.72	8.75	**8.85**
		biomass	6.23	6.40	6.81	6.92	6.96
	Spr/Aut	cover+biomass	3.10	3.32	3.36	3.48	3.55
		cover	3.38	3.44	3.53	3.59	**3.61**
		biomass	2.67	2.90	2.93	3.01	3.08
	Winter	cover+biomass	**3.48**	3.32	3.41	3.35	3.34
		cover	3.40	3.27	3.34	3.28	3.27
		biomass	3.07	3.02	3.07	3.03	3.02

Tab. I.4 Mean R^2 (in percent) for models explaining the effect of cover and biomass on variation in site selection (deviation from random choice) over **time of year**. The higher the R^2, the more accurate the prediction of a new data set (using 5-fold cross-validation). nk refers to the number of basis functions used to build the spline, which equals the number of parameters estimated for each variable. For each time of day (day, twilight, night) three models were estimated including either cover, biomass, or both as explanatory variables for site selection. Different flexibilities (nk) of the spline modelled the variation in the coefficient over time of year. In the linear case there was no variation, and a constant selection of cover or biomass, over year was assumed, respectively. Null deviation is based on a model where each proposed location in one step was assigned the same probability. Bold values refer to the highest value of R^2.

Sex	Daytime	Variables	const	nk=3	nk=4	nk=5	nk=6
males	day	cover+biomass	2.724	3.071	3.563	3.556	**3.577**
		cover	2.622	2.972	3.464	3.454	3.448
		biomass	2.726	2.830	2.955	2.958	2.958
	twilight	cover+biomass	2.204	2.540	4.043	**4.218**	4.213
		cover	2.217	2.473	3.927	3.931	3.933
		biomass	2.044	2.215	3.195	3.300	3.325
	night	cover+biomass	5.650	6.059	7.531	7.523	**7.583**
		cover	5.711	6.037	7.300	7.285	7.239
		biomass	5.604	5.889	6.953	6.978	6.979
females	day	cover+biomass	3.499	3.662	4.310	4.282	4.388
		cover	3.495	3.659	4.393	4.394	**4.415**
		biomass	3.424	3.478	3.742	3.754	3.739
	twilight	cover+biomass	2.493	2.938	4.904	4.768	4.729
		cover	2.781	3.137	4.957	4.899	**4.975**
		biomass	2.131	2.477	3.511	3.408	3.418
	night	cover+biomass	4.019	4.439	6.292	6.287	6.334
		cover	4.422	4.709	**6.653**	6.592	6.648
		biomass	3.854	4.239	5.283	5.231	5.293

Supplementary material

Appendix 1: Study area

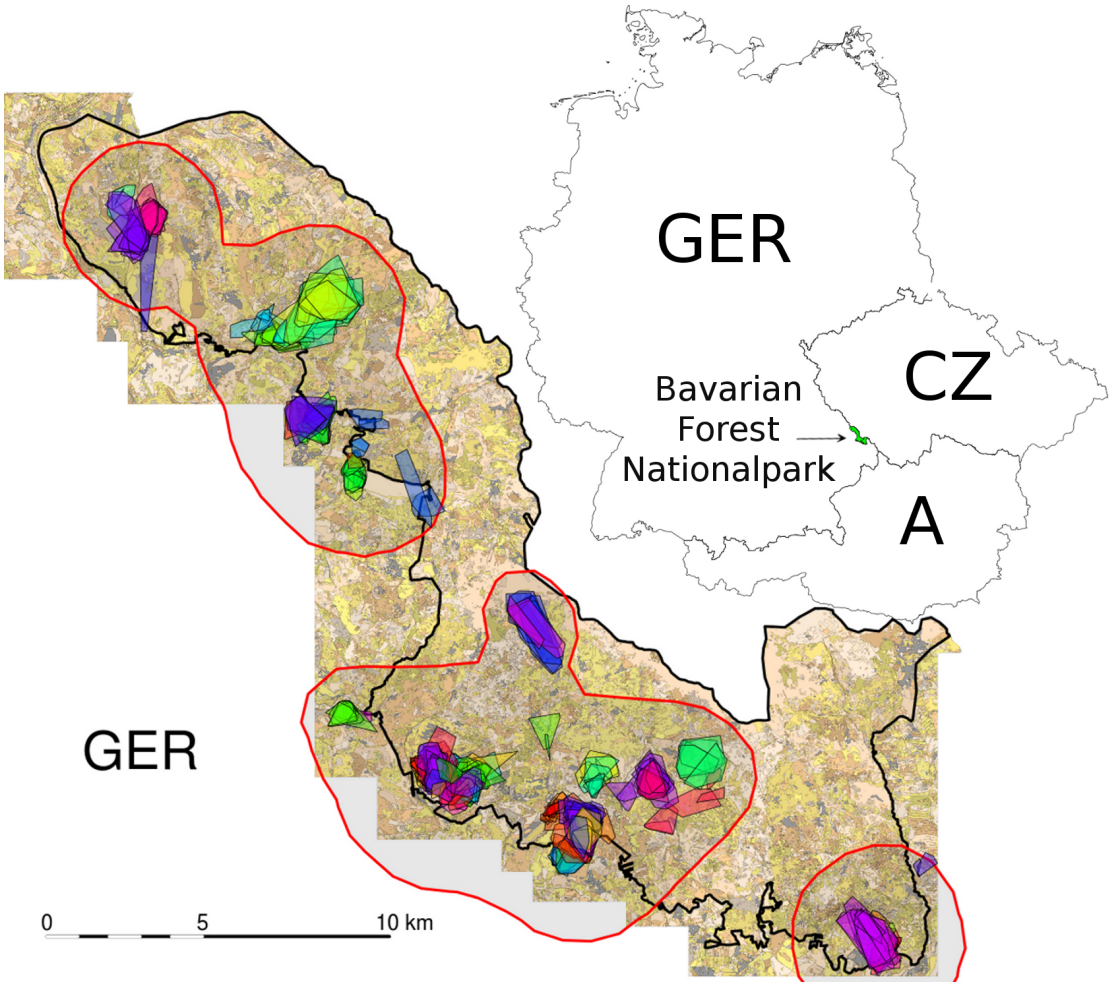

Fig. A1 The Bavarian Forest National Park (yellow) is situated in south-east Germany. Polygons show the monthly home ranges of the 52 adult roe deer (26 males, 26 females) used in this study, and each colour represents one individual. Monthly home ranges were used to caluclate the monthly availabilities of habitats. Availability on the larger scale was defined as the proportion of each habitat type within the red-bordered area.

Seasonal variation of forage availability and quality is strongly related to the vegetation period: in spring, biomass is dominated by high quality forage (Marell et al. 2009) while later in the growing season a large quantity of biomass guarantees availability of palatable plants. In deciduous and mixed forests, ground plant growth can be massively suppressed after foliation. In autumn high-energy beechnuts are abundant (Olesen and Madsen 2008). During winter, only few palatable plants (*e.g.*, *Rubus spp.*, tree regeneration) are available. Vegetation cover and its impact on predation risk changes with season. In forest habitats, leaves of tree regeneration offer cover from spring to autumn, while on unmanaged meadows, dense and well-developed ground vegetation of late-spring and summer maximize cover.

Appendix 2: Handling autocorrelation

The two analyses, i.e. monthly habitat selection and resource step selection, make different assumptions about the time scale over which successive locations are (conditionally) independent. Variograms can be used both to illustrate the two time scales and to identify the corresponding time scales for a given data set (Fleming et al. 2014). For the monthly habitat selection, it was assumed that successive locations are independent at the scale of the home range, i.e. that the animal might have crossed the home range between successive steps. In the variogram, this condition is found at the time interval between successive steps where the squared displacement distance (approximately) levels off. Step selection functions make less strict assumptions; they simply assume that successive steps are conditionally independent, in particular, that the speed of successive steps is uncorrelated. In the variogram, this condition is found at the time interval where the variogram starts to become linear after an initial concave phase. Variograms were displayed using the package ctmm (Fleming and Calabrese 2015). We visually inspected the short lag behaviour and long range behaviour of each individual.

Appendix 3: Large-scale analysis

We compared the availability and the use of habitat types based on the methodology used by McLoughlin et al. (2007), computing selection coefficients. Habitat availability at the landscape scale was defined as the proportion of the different habitat types in the area covered by the 90% utilization distribution kernel of all locations of all roe deer (red bordered polygons in Fig. A1). This area defines the composition of habitats in the immediate surrounding of the most frequented places by recorded roe deer. Habitat use for a given deer was defined as the proportion of a habitat in its monthly 95% minimum convex polygon home range for each individual and month (coloured polygons in Fig. A1). Here we aimed to define the area that is theoretically available to the animal, yet it includes areas that are not used. Monthly selection indices for home ranges were then calculated as: $w_i = \frac{u_i}{a_i}$ where u_i is the proportion of habitat i in the home range of an individual and a_i the proportional availability in the surrounding of all individuals. The selection indices were standardized to $B_i = \frac{w_i}{\sum_j w_j}$. So that B_i can be interpreted as the probability that habitat i is selected by an individual given that all habitat types are equally available to the individual (McLoughlin et al. 2007). The analyses was conducted separately for females and males. Results are shown in Figs. A2 & A3. For 11 habitat types a random selection (no preference) would mean $B_i = 1/11 = 0.09$. Variation of the proportions over the seasonal scale was modelled by a generalized additive mixed model with a individual-specific random effect and a beta distribution with a logit link (Wood 2006).

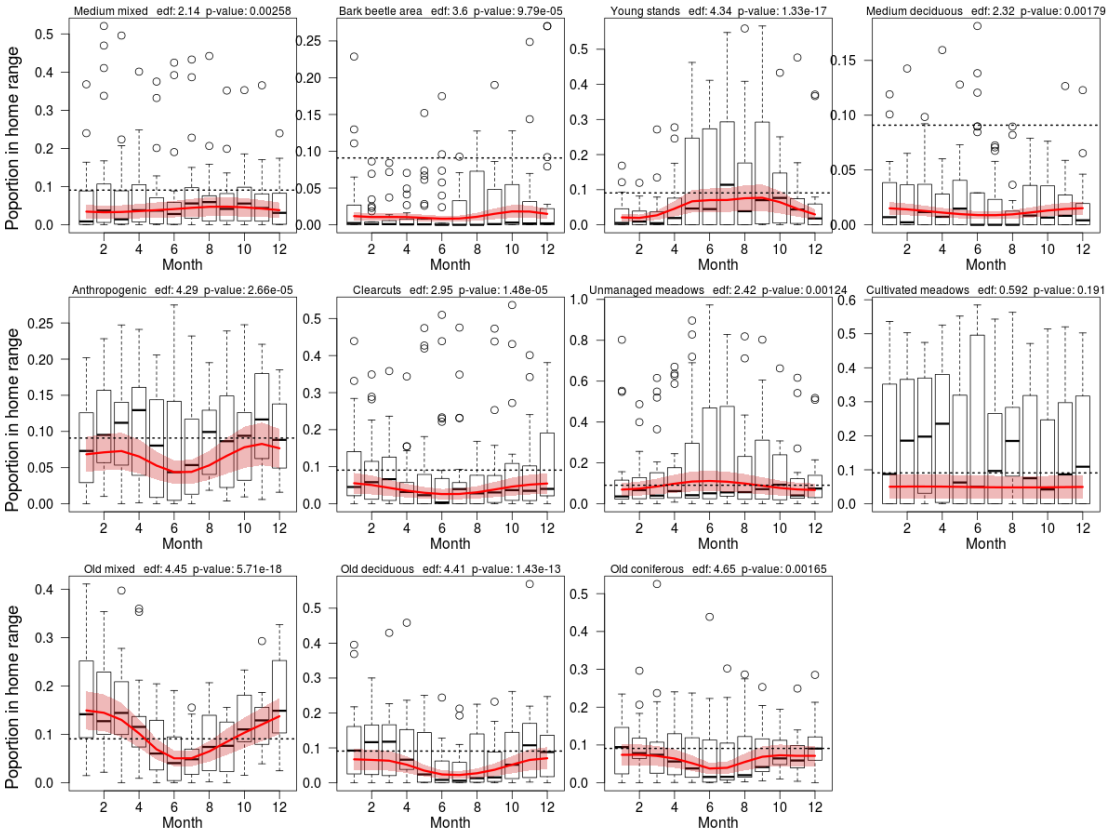

Fig. A2 Variation of the probability that a habitat is selected by the individual over the seasonal scale for females at the second order scale of selection (sensu Johnson 1980), i.e. by comapring the home-range composition with the composition of the landscape. Boxplots show the calculated selection probabilities for all individuals. The graph was modelled by a generalized additive model and show the predicted mean and the 95 percent confidence interval. Horizontal dotted line at 0.09 (1/11) refer to a selection that would indicate random choice. edf are the estimated degrees of freedom of the smoother. The p-value refers to the significance of the smoother.

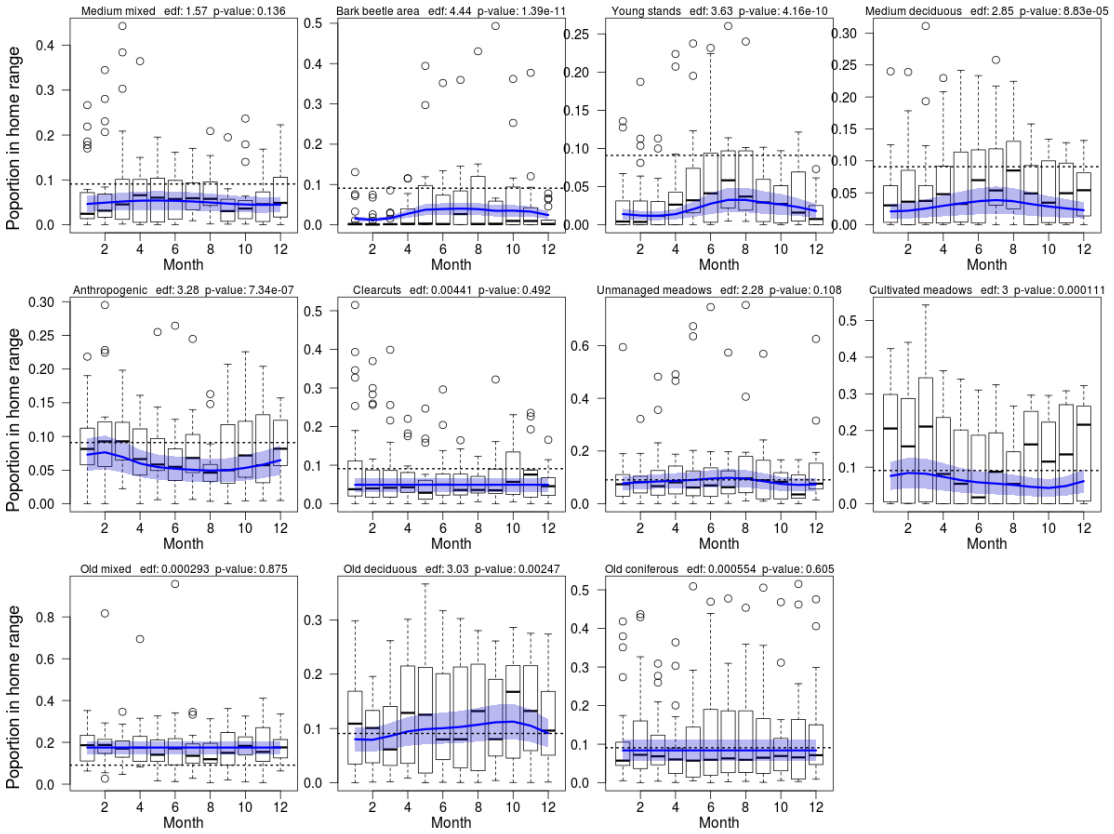

Fig. A3 Variation of the probability that a habitat is selected by the individual over the seasonal scale for males at the second order scale of selection (sensu Johnson 1980), i.e. by comapring the home-range composition with the composition of the landscape. Boxplots show the calculated selection probabilities for all individuals. The graph was modelled by a generalized additive model and show the predicted mean and the 95 percent confidence interval. Horizontal dotted line at 0.09 (1/11) refer to a selection that would indicate random choice.

Appendix 4: Model selection process for multicategory models

In total, we fitted 6 different models for each habitat type (Fig. 1). To account for the problem of overfitting, we measured the prediction accuracy of all the models by applying a cross-validation. Model predictive accuracy was obtained for each habitat separately. To apply cross-validation we split the data into five subgroups, ensuring that: (*i*) the data for each individual was evenly spread over all 10 groups; and (*ii*) within the groups, the data for all times of the year and day were available. In each of the five runs, four of the subgroups were used to estimate model coefficients which were applied to predict the outcome of the remaining 5th group. Because the prediction is a probability and the observed variable is binary, a receiver operating characteristic (ROC) curve was used for model selection (Pearce and Ferrier 2000, Agresti 2002, Boyce et al. 2002). The values of the area under the curve (AUC) were calculated and averaged over the five runs. For the calculation of the ROC curves and AUC values we used the package *ROCR* (Sing et al. 2005). The higher the AUC value, the higher the predictive accuracy of a model (Pearce and Ferrier 2000). Predictive accuracy refers to the selection choice between a habitat and the reference type, which in our case is the old mixed stands. That means that the more strongly the use of a habitat type differs compared to the use of the reference type, with respect to the model variables, the better is the predictive accuracy.

Appendix 5: Model selection process for SSF

The software we used does not provide any goodness of fit or model selection criteria for mixed conditional logistic regression models. Therefore, the most parsimonious model was found by applying 5-fold cross-validation (Boyce et al. 2002). Here, we used only 5-fold, to ensure that each fold contained sufficient data to calculate selection over both time scales. Given a model M, we first estimated the coefficient of a subset (4/5) of the whole data set. We did not include any random effects because individuals were not evenly spread over the folds. Given the estimated coefficients, probabilities for all locations for each step were calculated for the $1/5$ subset remaining. The residuals on the response scale $r(M_k)$ for the k-fold were then calculated. Residuals were then compared with the residuals of the Null Model $M0_k$, where each position had the probability of 1/(number of available locations in step i). We calculated $R^2_k = 1 - \sum r(M_k)/\sum r(M0_k)$.

Appendix 6: Temporal variation of habitat selection

Animation: Animation shows selection probability for all habitat types over time of day running over time of year estimated for 26 male (left) and 26 female(right) roe deer in the Bavarian Forest National Park, Germany recorded from 2002 to 2011. Estimates were based on the average availability over all animals (males and females separately), shown at the rear of the plots.

Appendix 7: Estimated selection coefficients

Selection coefficients are estimated for each habitat type at the third order scale of selection, for different times of day (0h, 4h, 8h, 12h, 16h, 20h), for different months (January, April, July, October) separated for females (f) and males (m) based on cyclic gamms.

January	0h		4h		8h		12h		16h		20h	
	f	m	f	m	f	m	f	m	f	m	f	m
Old mixed	0.30	0.25	0.27	0.13	0.31	0.12	0.35	0.24	0.39	0.40	0.39	0.41
Bark beetle area	-1.08	-1.57	-0.59	-0.95	-0.34	0.31	0.32	0.58	-0.41	-0.36	-1.75	-1.34
Unmanaged meadows	-0.55	-0.28	-0.84	-0.60	-1.61	-0.94	-1.69	-0.98	-1.16	-0.64	-0.73	-0.28
Cultivated meadows	0.17	-0.24	0.27	0.22	-1.40	-0.92	-3.22	-2.54	-2.69	-2.26	-0.70	-0.82
Clearcuts	-0.59	-0.78	-0.59	-0.70	-0.59	-0.67	-0.59	-0.74	-0.59	-0.84	-0.59	-0.85
Young stands	-1.29	-1.12	-1.09	-0.91	-0.79	-0.46	-0.63	-0.32	-0.81	-0.66	-1.17	-1.06
Old deciduous	-0.19	-0.15	-0.19	-0.15	-0.24	-0.15	-0.27	-0.15	-0.26	-0.15	-0.22	-0.15
Old coniferous	-0.28	0.07	-0.19	0.27	0.13	0.44	0.31	0.37	0.12	0.13	-0.19	-0.01
Medium mixed	-0.76	-0.39	-0.76	-0.29	-0.37	0.24	0.06	0.51	-0.17	0.17	-0.73	-0.28
Medium deciduous	-0.03	-0.02	-0.30	-0.02	-0.52	-0.02	-0.56	-0.02	-0.37	-0.02	-0.08	-0.02
Anthropogenic	0.56	0.58	1.06	1.11	0.08	0.45	-0.71	-0.60	-0.76	-1.03	-0.35	-0.46

Table A1 Estimated selection coefficients for January for different times of day for females (f) and males (m).

April	0h		4h		8h		12h		16h		20h	
	f	m	f	m	f	m	f	m	f	m	f	m
Old mixed	0.12	0.07	0.14	0.17	0.21	0.33	0.23	0.40	0.23	0.33	0.19	0.16
Bark beetle area	-1.75	-1.41	-1.80	-1.20	-0.59	-0.01	0.99	0.82	1.00	0.47	-0.61	-0.63
Unmanaged meadows	0.85	0.67	0.38	0.15	-0.60	-0.58	-1.03	-0.78	-0.53	-0.36	0.38	0.32
Cultivated meadows	0.53	1.01	-0.22	0.38	-1.31	-1.52	-2.26	-2.78	-1.77	-2.04	-0.09	-0.05
Clearcuts	-0.43	-0.13	-0.43	-0.12	-0.43	-0.18	-0.43	-0.25	-0.43	-0.26	-0.43	-0.20
Young stands	-0.77	-0.28	-0.65	-0.48	-0.36	-0.31	-0.17	-0.17	-0.28	-0.11	-0.60	-0.08
Old deciduous	-0.13	-0.15	-0.10	-0.15	-0.11	-0.15	-0.13	-0.15	-0.15	-0.15	-0.14	-0.15
Old coniferous	-0.18	-0.24	-0.10	-0.29	0.18	-0.28	0.33	-0.21	0.15	-0.14	-0.12	-0.14
Medium mixed	-0.84	-0.48	-0.78	-0.56	-0.06	-0.24	0.67	0.08	0.41	0.07	-0.51	-0.20
Medium deciduous	0.48	-0.10	0.16	-0.10	-0.13	-0.10	-0.16	-0.10	0.13	-0.10	0.47	-0.10
Anthropogenic	0.75	0.58	0.80	1.12	-0.26	0.46	-0.84	-0.59	-0.61	-1.03	-0.00	-0.46

Table A2 Estimated selection coefficients for April for different times of day for females (f) and males (m).

July	0h		4h		8h		12h		16h		20h	
	f	m	f	m	f	m	f	m	f	m	f	m
Old mixed	-0.66	-0.62	-0.52	-0.47	-0.33	-0.24	-0.30	-0.14	-0.44	-0.24	-0.61	-0.47
Bark beetle area	1.03	-0.03	0.53	-0.12	1.11	0.82	2.28	1.65	2.64	1.50	1.88	0.68
Unmanaged meadows	2.48	1.51	1.61	1.07	0.73	0.60	0.71	0.58	1.28	0.74	2.05	1.11
Cultivated meadows	3.26	3.28	2.26	2.12	0.68	-0.05	0.71	-1.27	1.49	-0.68	2.39	1.59
Clearcuts	1.10	1.01	1.10	1.01	1.10	0.94	1.10	0.85	1.10	0.86	1.10	0.94
Young stands	0.88	0.00	0.92	0.12	1.23	0.98	1.50	1.46	1.47	1.29	1.16	0.69
Old deciduous	0.44	0.25	0.45	0.25	0.45	0.25	0.45	0.25	0.44	0.25	0.44	0.25
Old coniferous	-0.30	0.12	-0.26	0.00	0.02	0.02	0.21	0.16	0.13	0.28	-0.12	0.26
Medium mixed	0.12	-0.53	0.16	-0.59	0.66	-0.03	1.20	0.62	1.19	0.67	0.61	0.07
Medium deciduous	0.30	0.12	0.25	0.12	0.44	0.12	0.67	0.12	0.72	0.12	0.54	0.12
Anthropogenic	1.24	0.58	1.30	1.11	-0.08	0.45	-0.95	-0.60	-0.74	-1.03	0.14	-0.46

Table A3 Estimated selection coefficients for July for different times of day for females (f) and males (m).

October	0h		4h		8h		12h		16h		20h	
	f	m	f	m	f	m	f	m	f	m	f	m
Old mixed	-0.18	-0.36	-0.14	-0.38	-0.09	-0.30	-0.11	-0.21	-0.15	-0.13	-0.17	-0.18
Bark beetle area	-0.31	-0.28	-0.50	0.05	0.22	1.18	1.71	1.59	1.43	0.84	-0.15	-0.03
Unmanaged meadows	1.02	0.68	0.52	0.39	-0.40	-0.15	-0.44	-0.41	0.10	-0.29	0.62	0.21
Cultivated meadows	1.77	2.30	1.22	2.06	-1.45	-0.21	-2.24	-2.01	-0.70	-1.43	0.94	0.78
Clearcuts	0.80	0.80	0.80	0.85	0.80	0.84	0.80	0.78	0.80	0.72	0.80	0.73
Young stands	0.03	-0.68	0.21	-0.08	0.85	1.10	1.37	1.54	1.23	0.87	0.51	-0.20
Old deciduous	0.33	0.37	0.33	0.37	0.30	0.37	0.28	0.37	0.28	0.37	0.31	0.37
Old coniferous	-0.44	-0.45	-0.38	-0.30	-0.04	0.01	0.20	0.15	0.10	-0.05	-0.21	-0.35
Medium mixed	-0.45	-0.50	-0.21	-0.39	0.51	0.39	1.10	1.01	0.86	0.74	-0.00	-0.06
Medium deciduous	-0.20	0.18	-0.26	0.18	-0.10	0.18	0.09	0.18	0.12	0.18	-0.02	0.18
Anthropogenic	1.01	0.57	1.52	1.10	0.22	0.44	-0.84	-0.61	-0.91	-1.04	-0.23	-0.46

Table A4 Estimated selection coefficients for October for different times of day for females (f) and males (m).

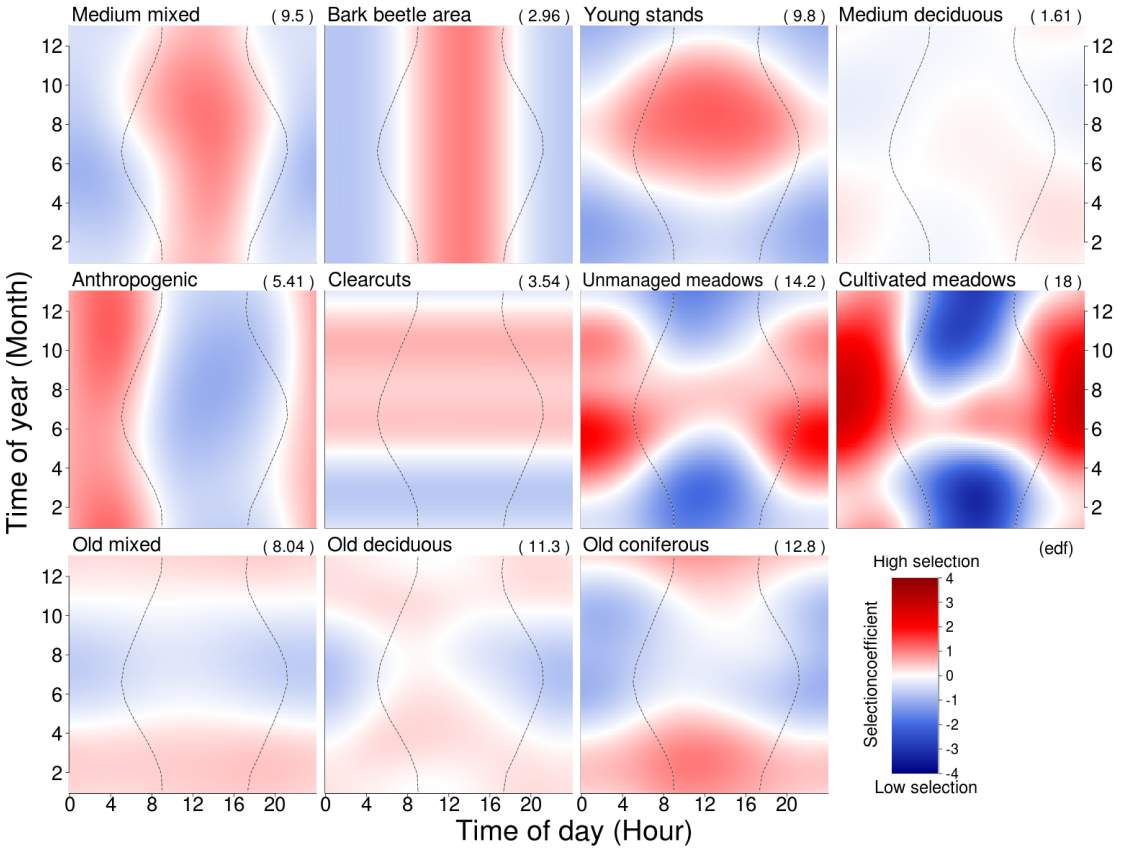

Fig. A4 Habitat selection on 3rd order (within home range): Variation of the selection coefficient over time of year (y-axis) and day (x-axis) for 17 **female** roe deer in the Bavarian Forest National Park, Germany recorded from 2002 to 2011. Colour indicates the value of the selection coefficient for the respective land-cover type. Estimated degrees of freedom (edf) refers to the "wiggliness" of the smooth.

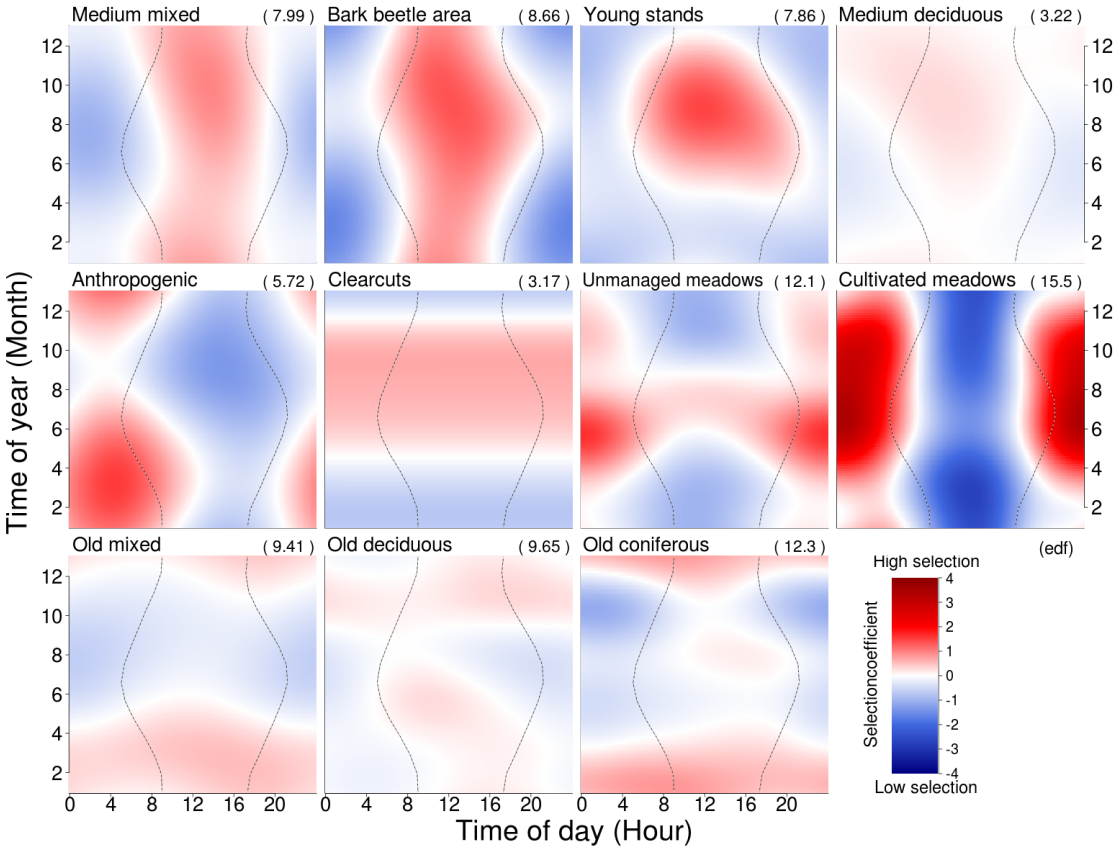

Fig. A5 Habitat selection on 3rd order (within home range): Variation of the selection coefficient over time of year (y-axis) and day (x-axis) for 19 **male** roe deer in the Bavarian Forest National Park, Germany recorded from 2002 to 2011. Colour indicates the value of the selection coefficient for the respective land-cover type. Estimated degrees of freedom (edf) refers to the "wiggliness" of the smooth.

Appendix 8: Uncertainties of selection coefficients

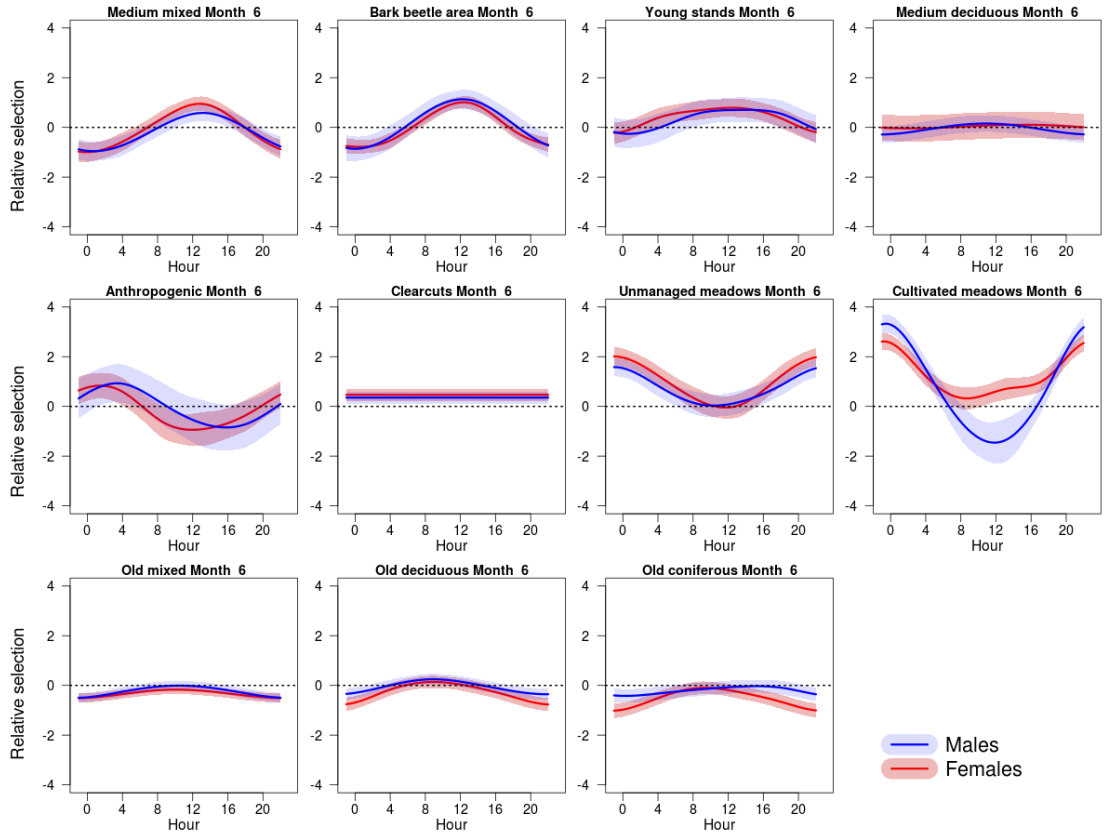

Fig. A6 Estimated selection coeffients over the diurnal scale in June for all habitats with 95% confidence intervals for females (red) and males (blue).

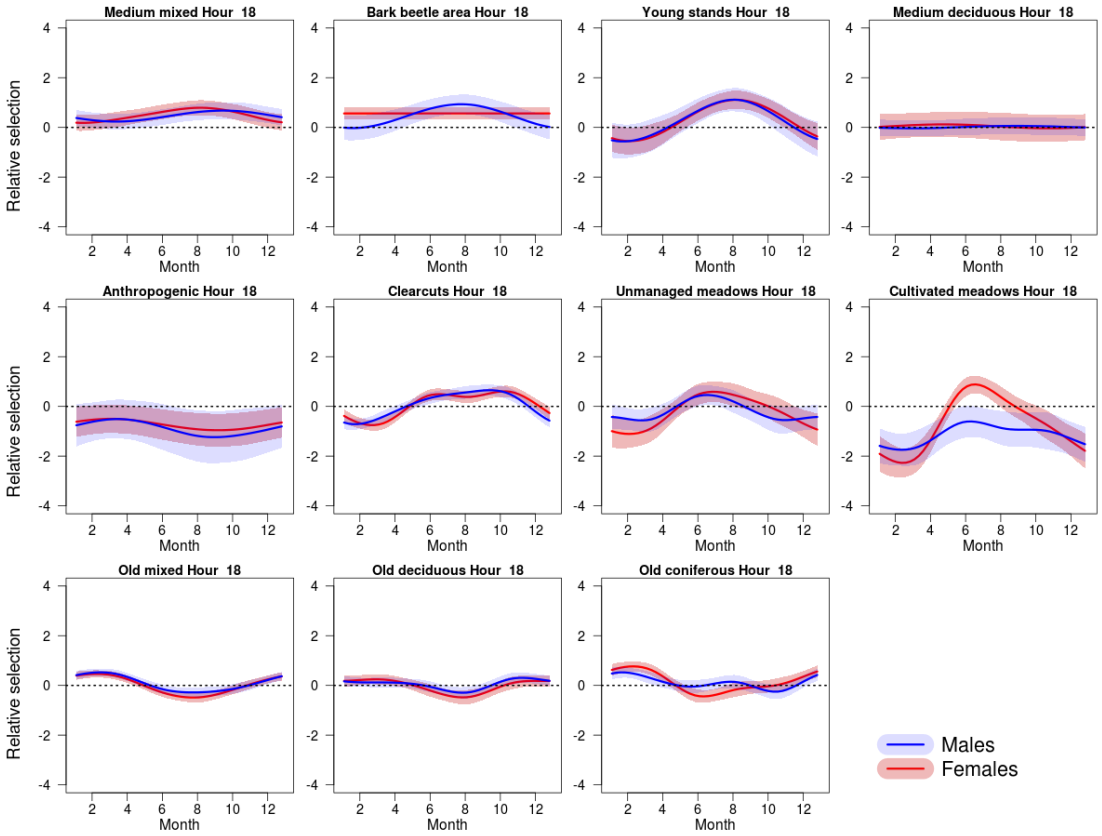

Fig. A7 Estimated selection coeffients over the seasonal scale at 6pm for all habitats with 95% confidence intervals for females (red) and males (blue).

Appendix 9: Comparison of three different sampling designs in the SSF framework

Methods

The definition of available habitat to the animal can strongly affect the outcome of habitat selection analyses (see also Northrup et al. 2013). We compared three different designs that differ in how random control location are drawn. We sampled 10 different control location around each observed location by using three different distributions for drawing step lengths and turning angles.

1. **pooled**: distributions are based on **empirical** samples of step-length and turning angles for all times; meaning two distributions for all time periods only separated for the two sexes;
2. **time-varying**: distributions are time-specific and based on **empirical** samples of step-length and turning angles for different time periods (defined by season and photoperiod/time of day); meaning six distributions for each of the two sexes;
3. **parametric**: we used an exponential distribution for step lengths with parameter λ equals twice the sample mean of observed step lengths and an uniform distribution for turning angles (Forester et al. 2009); the movement behaviour, namely the absolute turning angle and time-varying step length is included in the parameter estimation process.

Season is defined as Winter (December–March), Summer (May–Sep), Spring/Autumn (Apr, Oct, Nov)

All analyses were conducted in **R** version 3.1.3 (R Core Team 2015) using the packages mgcv version 1.7-22. (Wood 2006) for GAMMs, adehabitatLT version 0.3.5 for home range calculations (Calenge 2006), and xtable version 1.7-0. (Dahl 2012) for exporting tables.

Results

Description of the AUC tables We present the mean R^2 (in percent) for all models with varying numbers of covariates (cover, biomass or cover and biomass) and different degress of flexibilies for explaining the variation of coefficients over time of day and time of year. Models explain the effect of cover and biomass on variation in site selection (deviation from random choice). The higher the R^2, the more accurate is the prediction on a new data set (using 5-fold cross-validation). *nk* refers to the number of basis functions used to build the spline, which equals the number of parameters estimated for each variable. For each season (summer, spring/autumn, winter), for each time of day (day, twilight, night), three models were estimated, including either cover, biomass, or both as explanatory variables for site selection. Different flexibilities (*nk*) of the spline modelled the variation in the coefficient over time of day. In the linear case (*const*) there was no variation and a constant selection of cover or biomass over years was assumed, respectively . Null deviation is based on a model where each proposed location in one step was assigned the same probability. Bold values refer to the highest value of R^2.

The models with the highest R^2 are shown in the figures and can be compared between the different sampling designs.

Description of the figures showing predictions of the model Variation in the selection coefficient for cover (left) and biomass (right) over time of year and day for 21 male (blue lines) and 20 female (red lines) roe deer recorded from 2002 to 2011 in the Bavarian Forest National Park, Germany during the daytime (dashed line) and nighttime (solid line), based on step selection functions. Shaded areas indicate the 95pointwise confidence limits.

Diurnal variation The results of the cross-validation for different designs support always models with the same combinations of variables (Tab. A5). For males models that include both variables, biomass and cover, have always the highest R^2. For females in summer and spring/autumn models including only cover have the highest predictive rate. For winter for males, models that include both variables are most strongly supported. However, the degree of variation over time differs, meaning that splines with a different number of knots and therefore with different flexibility are supported. Between the design with pooled distributions and the design with parametric distributions only variation over time of day for males in winter differs. Here, for the parametric version slight variation is supported, whereas for the pooled design a model with no variation is found to be the best. However, the design with time-varying distributions differs for males in summer and spring/autumn supporting a lower flexibility of splines. Within this design also a model with a constant selection of cover and biomass over the course of the day is supported for males in winter.

Predicted patterns of the models are very similar for the pooled and the parametric designs (Tab. A7). The only strong difference can be detected for males in winter. In general, in winter cover is strongly selected throughout the day, found for all designs (estimated selection coefficient for females in all designs: ≈ 1.3). Only in the paramteric version, for males a time-variation in winter is detected, with a higher selection during daylight hours (max:1.7) than during night (min:0.6). A higher selection of cover during daylight than during nighttime is found for summer and autumn/spring for females and males. However, the rate of change was always higher for the pooled and the parametric design than for the time-varying design (e.g. for females in summer maximum and minimum selection coefficient for pooled design: -0.6 and -3.5, for time-varying design: -1.1 and -2.9)

Alteration of the selection of biomass over the course of day was less pronounced than the variation of selection of cover. For females, biomass does not influence site selection of roe deer at all in summer and autumn/spring. In winter biomass is selected with a constant rate throughout the day, which is about the same (≈ -0.4) for all designs. For males, variation of the selection of biomass in summer and Autumn/Spring showed a minimum selection during twilight hours, with a little peak during noon and a high peak during night hours. As the time-varying design supported a model with lower flexibility, only one minimum during noon and one maximum at midnight can be detected.

Seasonal variation Supported models match in the combination of variables and the degree of flexibility over the course of the year for almost all times of day between the pooled and the parametric design (Tab. A6). The only difference is found for females during the day. While in the pooled (and time-varying) version a combination of cover and biomass with the highest flexibility is supported, in the parametric version only cover with the highest flexibility is included in the most predictive model. Supported models in time-varying design differed only for males

during twilight and females during the day by a lower flexibility of the variation of selection of biomass and cover throughout the year.

For all designs the patterns of temporal variation of selection of cover and biomass equals (Tab. A7). Cover is highly selected during winter for all times of the day (e.g. females at night for pooled design: 1.2, time-varying: 1, parametric: 1.6), whereas the selection is lowest during the summer months. For night this seasonal pattern is most pronounced even more strongly for females than for males, yielding the lowest selection coefficients (for pooled design: -4.3, time-varying: -3.5, parametric: -3.9). There are hardly any differences in the prediction of the three designs considering the selection of biomass over the seasonal scale by males. Biomass is highly selected during the summer (Selection coefficient: 1.7) month and has its minimum in November/December (0.7). The only difference in the different designs is found for females as already explained earlier. Predictions of the selection of biomass can therefore only compared for seasonal variation during the night, which shows a maximum during summer (pooled: -2, time-varying: -0.5). In the pooled design there is another local maximum (-0.6) in January, which is due to the higher complexity of the spline function. The minimum for the pooled version is in March/April (selection coefficient: -1.2), whereas the minimum for the time-varying design is in February (-1.6).

Discussion

For all designs we use the very same "present" locations. Only the sets of proposal locations are different which the "present" locations are contrasted with.

In the time-varying design the proposal locations are drawn from different distributions for each time slot, e.g. during day proposal locations are close to present location and therefore, given spatial auto-correlation, tend to be similar in environmental conditions. Hence, when present location will be compared to similar locations in terms of biomass and cover, selection will be estimated to be weak. Indeed, estimated coefficients in the time-varying design are in general closer to 0 than estimated values of the pooled and parametric design.

In the pooled and parametric designs proposal locations are drawn from one distribution for all times. Proposal locations represent what is theoretically available to the individual. Distributions of both designs yield similar sets of proposal locations. However, when estimating selection coefficients, the parametric design also accounts for temporal patterns of movement behaviour, meaning that part of the explanation why the animal has chosen the particular present location is explained by movement variables such as step lengths and turning angle, leaving less proportion of deviance to environmental factors such as biomass and cover. Therefore, in the parametric design estimated coefficients should be and are mostly marginally closer to 0 than in the pooled design (This is not always true, e.g. seasonal scale in winter). This is probably the reason why the selection of biomass over the course of the year by females was not significant different from 0. Out of the set of included variables, movement characteristics and availability of cover explains the difference between "present" and proposal location already. Biomass did not improve the model fit.

As the parametric design explicitely takes the temporal patterns in movement distances into account without limiting the set of proposal locations we favour this approach.

Pooled

Sex	Season	Variables	const	nk=3	nk=4	nk=5	nk=6
males	Summer	cover+biomass	1.37	1.43	1.97	2.08	**2.22**
		cover	1.5	1.45	1.82	1.88	2.00
		biomass	0.4	0.62	1.12	1.25	1.34
	AutSpr	cover+biomass	<0	0.18	0.34	0.42	**0.46**
		cover	<0	0.21	0.36	0.41	0.42
		biomass	<0	<0	0.14	0.22	0.25
	Winter	cover+biomass	**0.73**	0.63	0.72	0.67	0.67
		cover	0.68	0.6	0.66	0.64	0.64
		biomass	0.43	0.36	0.38	0.36	0.36
females	Summer	cover+biomass	<0	<0	<0	<0	2.58
		cover	<0	<0	<0	<0	**2.82**
		biomass	<0	<0	<0	<0	1.47
	AutSpr	cover+biomass	<0	0.6	0.65	0.74	0.77
		cover	<0	0.7	0.81	0.86	**0.87**
		biomass	<0	0.14	0.19	0.24	0.29
	Winter	cover+biomass	**1.15**	0.74	0.86	0.81	0.80
		cover	1.04	0.68	0.76	0.71	0.70
		biomass	0.72	0.48	0.54	0.52	0.52

Time-varying

Sex	Season	Variables	const	nk=3	nk=4	nk=5	nk=6
males	Summer	cover+biomass	0.25	0.24	**0.29**	0.27	0.25
		cover	0.25	0.24	0.25	0.24	0.23
		biomass	0	0.00	0.05	0.04	0.04
	AutSpr	cover+biomass	0.03	0.11	0.26	**0.35**	0.27
		cover	0.07	0.11	0.23	0.25	0.25
		biomass	<0	0.03	0.17	0.26	0.28
	Winter	cover+biomass	**0.44**	0.42	0.43	0.42	0.42
		cover	0.39	0.40	0.41	0.41	0.41
		biomass	0.22	0.21	0.21	0.20	0.20
females	Summer	cover+biomass	0.46	0.44	0.56	0.56	0.56
		cover	0.54	0.51	0.57	**0.57**	0.57
		biomass	0.12	0.15	0.24	0.25	0.25
	AutSpr	cover+biomass	0.15	0.23	0.28	0.35	0.37
		cover	0.31	0.35	0.38	0.40	**0.41**
		biomass	<0	0.02	0.07	0.10	0.12
	Winter	cover+biomass	**0.47**	0.42	0.41	0.39	0.39
		cover	0.43	0.39	0.38	0.36	0.36
		biomass	0.23	0.22	0.22	0.21	0.21

Parametric

Sex	Season	Variables	const	nk=3	nk=4	nk=5	nk=6
males	Summer	cover+biomass	2.87	2.91	3.51	3.63	**3.78**
		cover	3.05	2.97	3.31	3.35	3.51
		biomass	1.99	2.07	2.65	2.79	2.92
	AutSpr	cover+biomass	3.65	3.73	3.93	4.00	**4.06**
		cover	3.71	3.76	3.93	3.98	3.98
		biomass	3.46	3.49	3.66	3.75	3.81
	Winter	cover+biomass	6.56	6.53	**6.61**	6.58	6.60
		cover	6.46	6.46	6.51	6.48	6.50
		biomass	6.21	6.20	6.22	6.20	6.22
females	Summer	cover+biomass	7.70	7.84	8.39	8.46	8.54
		cover	8.29	8.26	8.72	8.75	**8.85**
		biomass	6.23	6.40	6.81	6.92	6.96
	AutSpr	cover+biomass	3.10	3.32	3.36	3.48	3.55
		cover	3.38	3.44	3.53	3.59	**3.61**
		biomass	2.67	2.90	2.93	3.01	3.08
	Winter	cover+biomass	**3.48**	3.32	3.41	3.35	3.34
		cover	3.40	3.27	3.34	3.28	3.27
		biomass	3.07	3.02	3.07	3.03	3.02

Table A5 AUC tables of models explaining diurnal variation in site selection for the three different sampling schemes.

Pooled

Sex	Daytime	Variables	const	nk=3	nk=4	nk=5	nk=6
males	day	cover+biomass	0.069	0.331	0.763	0.747	**0.788**
		cover	<0	0.242	0.681	0.659	0.670
		biomass	0.055	0.145	0.252	0.250	0.264
	twilight	cover+biomass	0.349	0.723	2.116	**2.309**	2.238
		cover	0.406	0.633	2.075	2.158	2.087
		biomass	0.183	0.399	1.347	1.440	1.512
	night	cover+biomass	0.163	0.542	1.879	1.908	**1.959**
		cover	0.224	0.491	1.665	1.654	1.652
		biomass	0.135	0.414	1.348	1.417	1.446
females	day	cover+biomass	0.063	0.237	0.775	0.761	**0.808**
		cover	0.018	0.194	0.779	0.797	0.797
		biomass	<0	0.051	0.308	0.317	0.307
	twilight	cover+biomass	0.633	1.205	2.535	2.449	2.508
		cover	0.898	1.377	2.746	2.696	**2.819**
		biomass	0.244	0.660	1.416	1.265	1.348
	night	cover+biomass	0.171	0.596	2.022	2.059	2.019
		cover	0.502	0.810	**2.368**	2.321	2.318
		biomass	0.01	0.328	1.213	1.200	1.216

Time-varying

Sex	Daytime	Variables	const	nk=3	nk=4	nk=5	nk=6
males	day	cover+biomass	0.011	0.022	0.033	0.025	**0.035**
		cover	<0	0.008	0.024	0.017	0.027
		biomass	0.009	0.009	0.002	0.001	0.002
	twilight	cover+biomass	0.351	0.481	**1.444**	1.357	1.405
		cover	0.384	0.385	1.100	0.893	1.089
		biomass	0.213	0.370	1.012	1.004	1.065
	night	cover+biomass	0.118	0.243	1.237	1.193	**1.217**
		cover	0.153	0.242	1.001	0.937	1.006
		biomass	0.085	0.164	0.819	0.828	0.848
females	day	cover+biomass	0.02	0.039	**0.075**	0.062	0.071
		cover	<0	0.010	0.048	0.040	0.063
		biomass	0.015	0.023	0.018	0.016	0.022
	twilight	cover+biomass	0.565	0.896	1.961	1.852	**2.114**
		cover	0.77	0.925	1.772	1.586	2.065
		biomass	0.237	0.434	1.037	0.881	1.193
	night	cover+biomass	0.108	0.280	1.548	1.483	1.537
		cover	0.315	0.415	**1.667**	1.545	1.661
		biomass	0.013	0.172	0.873	0.881	0.859

Parametric

Sex	Daytime	Variables	const	nk=3	nk=4	nk=5	nk=6
males	day	cover+biomass	2.724	3.071	3.563	3.556	**3.577**
		cover	2.622	2.972	3.464	3.454	3.448
		biomass	2.726	2.830	2.955	2.958	2.958
	twilight	cover+biomass	2.204	2.540	4.043	**4.218**	4.213
		cover	2.217	2.473	3.927	3.931	3.933
		biomass	2.044	2.215	3.195	3.300	3.325
	night	cover+biomass	5.650	6.059	7.531	7.523	**7.583**
		cover	5.711	6.037	7.300	7.285	7.239
		biomass	5.604	5.889	6.953	6.978	6.979
females	day	cover+biomass	3.499	3.662	4.310	4.282	4.388
		cover	3.495	3.659	4.393	4.394	**4.415**
		biomass	3.424	3.478	3.742	3.754	3.739
	twilight	cover+biomass	2.493	2.938	4.904	4.768	4.729
		cover	2.781	3.137	4.957	4.899	**4.975**
		biomass	2.131	2.477	3.511	3.408	3.418
	night	cover+biomass	4.019	4.439	6.292	6.287	6.334
		cover	4.422	4.709	**6.653**	6.592	6.648
		biomass	3.854	4.239	5.283	5.231	5.293

Table A6 AUC tables of models explaining seasonal variation in site selection for the three different sampling schemes.

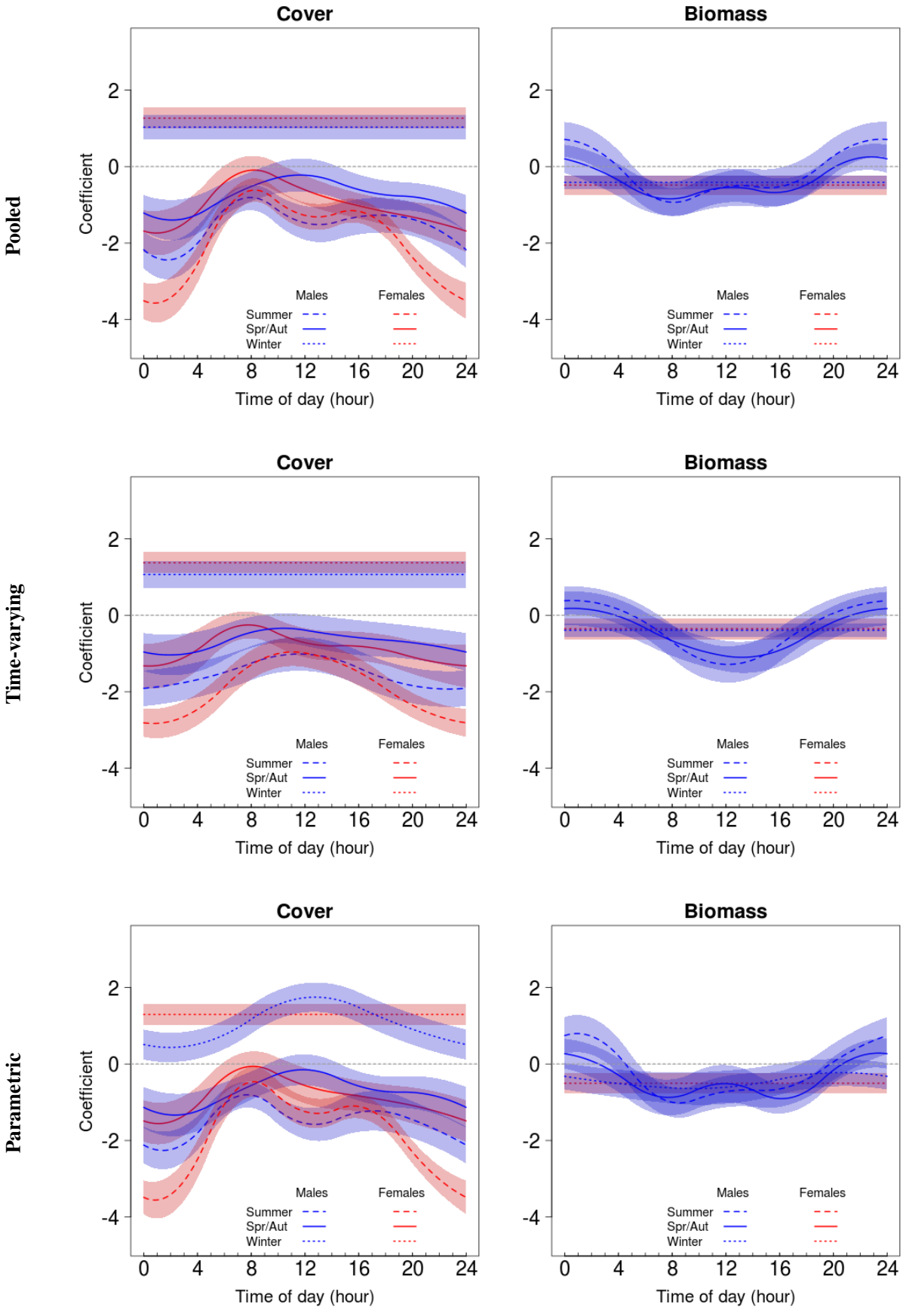

Table A7 Estimates of models explaining diurnal variation in site selection for the three different sampling schemes.

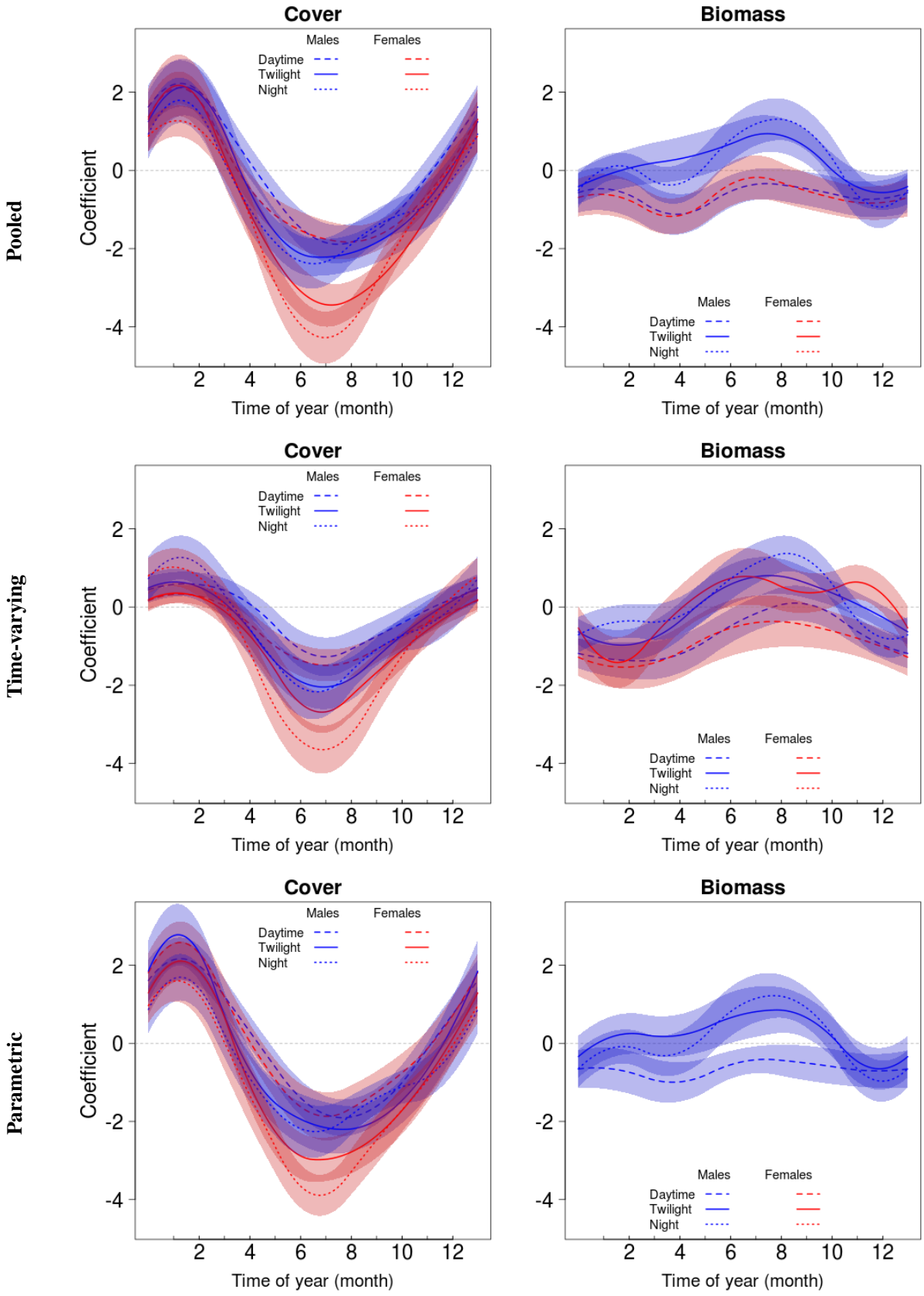

Table A8 Estimates of models explaining seasonal variation in site selection for the three different sampling schemes.

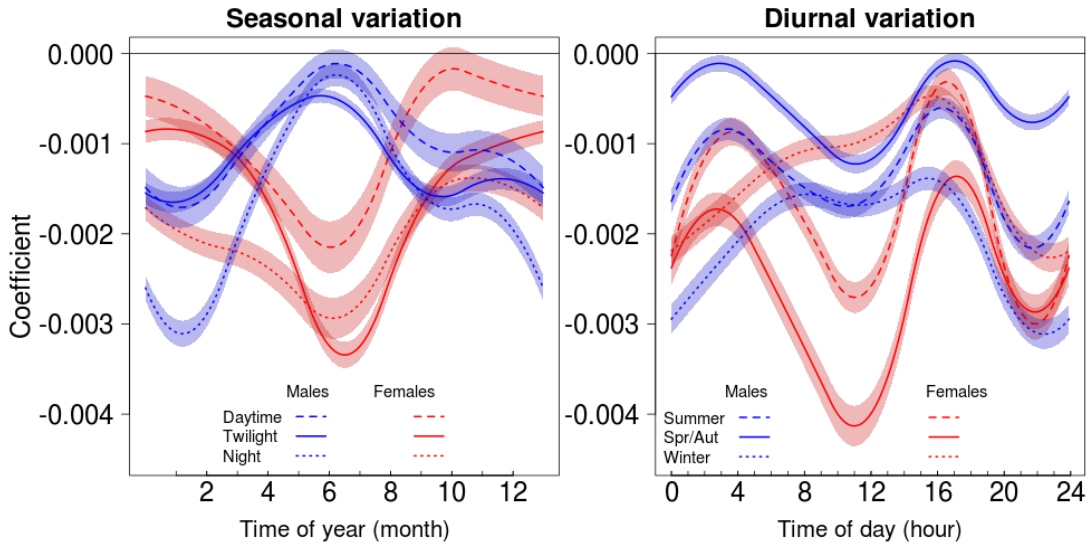

Fig. A8 Variation of the coefficient for step length over time of year (left) and time of day (right) for the parametric model.

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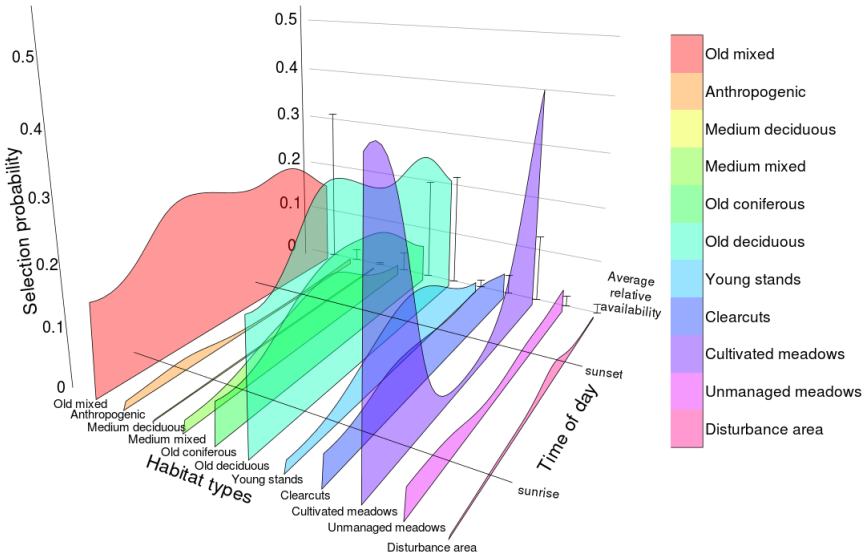


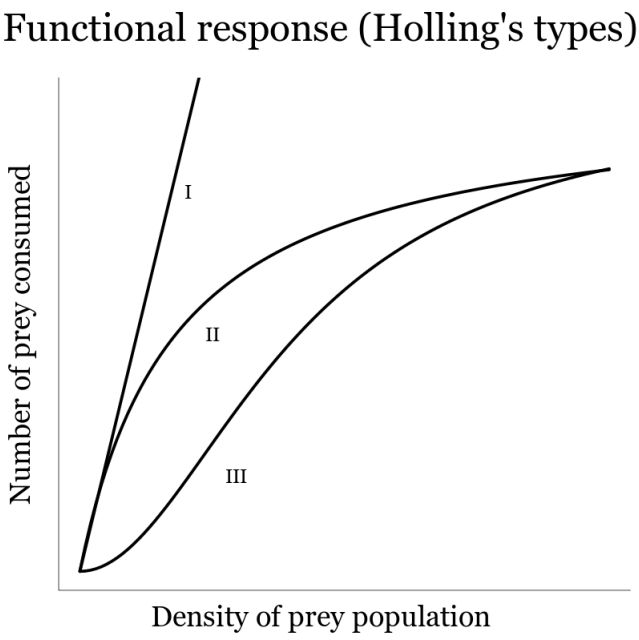
Figure 2.1: An animation in the attached material shows the selection probability for all habitat types over time of day running over time of year estimated for 19 male (left) and 17 female (right) roe deer in the Bavarian Forest National Park, Germany recorded from 2002 to 2011. Estimates were based on the average availability over all animals (males and females separately), shown at the rear of the plots.

Research paper II

Claudia Dupke, Marco Heurich, Björn Reineking, Christophe Bonenfant

Shape of functional response reveals strength of trade-off in resource use by a large herbivore

Summary: The selection of habitats is primarily driven by the internal needs of roe deer and to a lesser extent by the availability of habitats, given a fixed composition of habitats in the home range.



Authors affiliation:

Claudia Dupke*[1], Marco Heurich[2,3], Björn Reineking[1,4], Christophe Bonenfant[5]

[1] Biogeographical Modelling, Bayreuth Center of Ecology and Environmental Research BayCEER, University of Bayreuth, Universitätsstr. 30, 95440 Bayreuth, Germany

[2] Chair of Wildlife Ecology and Management, University of Freiburg, Tennenbacher Str. 4, 79106 Freiburg, Germany

[3] Department of Research and Documentation, Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany

[4] Université Grenoble Alpes, Irstea, UR EMGR 2 rue de la Papeterie BP 76, 38402 St-Martin-d'Héres, France

[5] Université de Lyon, F-69000, Lyon, Université Lyon 1, CNRS, UMR5558, Laboratoire de Biométrie et Biologie Évolutive, F-69622, Villeurbanne, France

* corresponding author

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Summary

1. Holling (1959) was the first who related a predator's consumption-rate with the density of its prey and called it functional response. This concept has been transferred to habitat selection of herbivores, where it was defined as the change in relative use with changing availability of habitats.

2. Functional response in habitat selection has been reported for several large herbivores at the home-range scale. However, none of these studies could link their observed patterns to Holling's types I, II or III, which may be due limitations of the used methodology.

3. We used discrete choice models implemented as mixed-effects baseline-category logit models to analyze variation of habitat selection of a large herbivore over seasonal and diurnal time scales. We investigated how habitat use varies with its availability in 11 habitat types used by roe deer in the Bavarian Forest Nationalpark, Germany.

4. We found strong evidence for non-linear functional responses for all 11 habitat types, which can be categorized as Holling's type I, II, III and even IV, with a predominance of type II. The shape of the functional response varies for females and males as well as with season and day / night.

5. We propose that functional response in habitat selection is the consequence of a trade-off in the use of habitats offering different resources by a herbivore that has temporally varying needs. Our results imply that mainly the animals' internal needs and to a lesser extent the availability of habitats determines habitat selection of animals, given a fixed composition of habitats within the home range.

Introduction

Holling (1959) first described for small insectivorous mammals the behavioural adjustments of carnivores according to the level of prey availability. Depending on the time required for searching, handling and consuming individual preys, three types of functional responses may arise describing linear (type I), concave (Type II) to a convex (type III) relationships between consumption and availability of preys by carnivores (Holling, 1959). It is assumed that specialist carnivores should have a type II functional response, *i.e.* the number of killed prey would increase rapidly with prey density and level off

when searching time and prey manipulation constrain predators in ability to consume more preys (Andersson and Erlinge, 1977). A generalist predator would instead show a slower increase, resulting in the sigmoid curve of a type III response Holling (1959) owing to changes in search image, foraging habitat or prey switching (Taylor, 1984). Such functional responses are well documented in large carnivores such as wolves (*Canis lupus,* Messier, 1994) or lynx (*Lynx lynx,* Nilsen et al., 2009).

For herbivores, functional responses were historically investigated at the bite level (Spalinger and Hobbs, 1992) to understand how much food animals could ingest and process with increasing resource availability. Past experimental work suggested that consumption of food is mainly governed by cropping and chewing times of plant parts in mammalian herbivores (Gross et al., 1995). Similar to carnivores, behavioural constraints will affect the ability of herbivores to find, select and process plant species or parts, generally leading to type II functional responses (Real, 1977). As defined by Holling (1959), functional responses take place at the finest scale of resource selection by animals (Johnson, 1980). However, resource selection is a hierarchical process, ranging from the fodder plant part to the species' geographical range. How food processing at the smallest scales of resource selection (level 3 or 4 according to Johnson, 1980) may scale-up to higher spatio-temporal scales such as home range and landscape levels (level 1 or 2 according to Johnson, 1980), and what behavioural adjustments or constrains such as on movement may occur currently lack understanding (but see Van Moorter et al., 2013).

Functional response in the sense of Holling (1959) relates the number of prey consumed to the density of prey. Transfered to habitat selection on the home range level, functional response becomes the function that relates the use of a habitat with its availability in the home range. In a seminal paper, Mysterud and Ims (1998) merged the concept of functional response with habitat selection behaviour at the home range scale (level 2 according to Johnson, 1980). They suggest that the underlying biological processes leading to functional responses in habitat selection are related to large-scale movements to reach the different habitat types, the search for particular resource patches within habitats, and the foraging and digestion process (Brown, 1999). Recently, an increasing number of empirical studies reported functional responses in several species of large herbivores at the home-range scale (moose (*Alces alces*): Bjørneraas et al., 2012); (caribou (*Rangifer tarandus*): Moreau et al., 2012) where most describe linear variations of selection strength with resource availability. For instance, red deer in western Norway selects the highly nutritive meadows relatively more often when its availability in the individuals' home range is low (Godvik et al., 2009). However, whether functional responses in habitat selection are general among large herbivores and how these functional responses vary in

time, among habitat types, with individual traits or environmental factors is not well understood. More importantly, the shapes of the functional responses for herbivores (*i.e.* non-linearity) have not been described in connection with Holling (1959)'s original curve typology.

Scarcity in studies of functional responses in large herbivores may partly lie in the methodology used to analyze habitat selection (McLoughlin et al., 2010; Beyer et al., 2010). A variety of methods are available to quantify habitat selection (Aebischer et al., 1993; Warton and Shepherd, 2010). But, over the last decade, resource selection functions (RSF, Manly et al., 2002) have been the most popular tool to link space use of animals to landscape characteristics by using the combination of case-control sampling and logistic regression (Duchesne et al., 2010; McLoughlin et al., 2010). However, associated issues with this approach are well-known, e.g. the way controls or "pseudo-absence" data are generated highly influence the model performance (Phillips et al., 2009; Warton and Shepherd, 2010; Warton and Aarts, 2013). Also, although commonly assumed, RSFs using logistic regression are not necessarily proportional to probability of use (Keating and Cherry, 2004). Nevertheless, RSFs were also applied to test for functional responses in habitat selection, where interaction terms between habitat type and habitat availability are usually presented or the effect of availability on odds ratios (Moreau et al., 2012; Godvik et al., 2009). Visualization of such a relationship obtained via RSF are difficult to understand as they do not directly show functional response but indications of it (e.g. Godvik et al., 2009) and are prone to misinterpretation (Beyer et al., 2010; Van Moorter et al., 2013). Therefore, alternative methods may be advised when dealing with functional responses in habitat selection such as multinomial logit discrete-choice models (Cooper and Millspaugh, 1999). These relate relative use to relative availability and account for the choice between multiple options. Finally, in spite of the flexibility of Generalized Additive Models (GAM, Hastie and Tibshirani, 1986) to investigate non-linear relationships between variables by smoothing-splines, GAMs have rarely been used in the context of habitat selection to explore functional responses (but see Bjørneraas et al., 2012).

Using $n > 15,000$ GPS locations on 36 free-ranging roe deer in the Bavarian Forest National Park, Germany, we first describe the selection pattern of 11 habitat types within the home range of individuals (second-order habitat selection) and its temporal variation at the daily and the monthly scales (Godvik et al., 2009; Herfindal et al., 2013). Specifically, we investigated how the selection of a particular habitat varies with its relative availability within the home-range (Mysterud and Ims, 1998). As repeatedly reported in large mammalian carnivores for their prey consumption (Messier, 1994), we predict

Tab. II.1 Overview of relative availability of habitat types in the study area, relative availability within the home ranges and relative use by roe deer in the Bavarian Forest National Park, in descending order of use.

Habitat	Avail. in study area	Avail. in home range	Use
Old deciduous	0.184	0.230	0.247
Old mixed	0.231	0.393	0.188
Old coniferous	0.220	0.188	0.170
Cultivated meadows	0.051	0.060	0.102
Medium mixed	0.075	0.045	0.079
Unmanaged meadows	0.020	0.014	0.064
Clearcuts	0.046	0.024	0.062
Young stands	0.020	0.009	0.047
Anthropogenic	0.027	0.022	0.018
Medium deciduous	0.015	0.007	0.014
Disturbance area	0.111	0.008	0.010

that non-linear relationship between the selection probability of a given habitat and its availability (Type II or III) is the rule over a proportional use (type I). Type II should be more pronounced in habitats providing specific resources, such as primarily forage on meadows. Because the costs-to-benefit ratio provided by the habitats and their selection intensity changes with season, we expected the functional response to differ with season (Godvik et al., 2009). Specifically, we expected the difference to be stronger for those habitats that are subjected to greater environmental changes between seasons.

Material and Methods

Study area

The study area is located in the Bavarian Forest National Park (BFNP), which lies in south-eastern Germany along the border to the Czech Republic (center coordinates $49\,°3'19''N, 13\,°12'9''E$). The BFNP has three major forest types structured along the altitudinal gradient. Above 1,100 m a.s.l. (16% of the area), sub-alpine spruce forests of Norway spruce (*Picea abies*) and some mountain ash (*Sorbus aucuparia*) prevail. On the slopes between 600 m and 1,100 m.a.s.l., mixed montane forests with Norway spruce, white fir (*Abies alba*), European beech (*Fagus sylvatica*) and sycamore maple (*Acer pseudoplatanus*, 68% of the area) are found (Heurich and Neufanger, 2005). Since the mid-1990s, the forests of the BFNP have been affected by massive proliferation of the spruce bark beetle (*Ips typographus*) which resulted in an dieback of old spruce trees totaling

an area of 7000 ha of disturbed forests(Heurich et al., 2010; Lausch et al., 2013). Spectrozonal aerial images of the study area from 2008 (Heurich et al., 2012*a*) were used to classify forest areas according to the land cover (Belyaev et al., 2004). Land cover was grouped into 11 classes (Tab. II.1). Management of roe deer in the BFNP is spatially limited to the wild ungulate management zone ($\approx 29\%$ of study area). This ensures that wildlife regulation is excluded from a core area of 7,000 ha (Möst et al., 2015). The estimated roe deer population density was low, ranging between 1-3 animals/km^2 (M. Heurich, unpublished data). During our study, roe deer in the BFNP was preyed upon by the European lynx (*Lynx lynx*) which had been reintroduced in the 1980s (Wölfl et al., 2001). Between 2005 and 2012, 168 individuals were monitored. 30% of these were killed by lynx, which is about 50% of mortality, 7% were killed in a road accident (Heurich et al., 2012*b*).

Roe Deer Capture and Radiotelemetry Data

We used wooden box traps to capture roe deer in the winter months. The animals were not chemically immobilized for attaching the neck-collar (Weilnböck et al., 2012). GPS-GSM collars (series 3.000) from VECTRONIC Aerospace, Berlin (Germany) recorded positions with different sampling intensities, ranging from every 3 min to every 12 h. For the analysis, only one location per hour was kept to reduce spatio-temporal autocorrelation. We also removed the first 10 days of each survey period to exclude a possible effect on behaviour owing to the capturing and handling of the animals (Morellet et al., 2009). For the analysis we excluded those animals whose fix success rate, defined as the number of successfully stored locations divided by the number of attempts (Frair et al., 2010), was below 90 percent. The averaged fix success rate of the remaining animals was then 97 percent. GPS errors were uniformly distributed across time of day ($\chi^2 = 0.04$, $df = 22$, $p > 0.999$) and time of year ($\chi^2 = 0.1$, $df = 10$, $p > 0.999$), we discarded missing values from the analysis (n=6,138).

We used a total of 172,507 fixes of 52 roe deer (26 males, 26 females) before thinning ranging from 136 to 17,044 fixes per individual (mean: 3,317, sd: 2,897) over a period from 14 to 2,081 days (mean: 484, sd: 397). The spatial accuracy of the fixes was 10 m on average with a maximum recorded error of 16.3 m (Stache et al., 2012).

Spatial autorcorrelation was analysed using variograms (Fleming et al., 2014). For the monthly habitat selection, it is assumed that successive locations are independent at the scale of the home range, i.e. that the animal might have crossed the home range between successive steps. In the variogram, this condition is found at the time interval

between successive steps where the squared displacement distance (approximately) levels off. Variograms were calculated using the package ctmm (Fleming and Calabrese, 2015). We visually inspected variograms of the long range behaviour of each individual. In our data this interval was approximately 25 h. We included only those individuals with more than 70 recordings. Our data set contained then n =15,267 locations of 17 females and 19 males.

Statistical methods

The multicategorical logit model

When considering site selection, individuals have the choice between different habitat categories (Tab. II.1). Multicategory logit models can be fitted using baseline-category logit models (Agresti, 2002). Following Agresti (2002), the habitat type with the highest prevalence was chosen as baseline, which in our case was the old mixed stand habitat type, used in 27% of all recorded positions. The probability of choosing the baseline category K was calculated as: $\pi_K(\boldsymbol{x}) = 1-\pi_1(\boldsymbol{x})-\ldots-\pi_{K-1}(\boldsymbol{x})$, where $\boldsymbol{x}$ is a vector of covariates describing the habitat and/or the individual and probabilities $\pi_i(\boldsymbol{x})$, $i = 1,\ldots,K-1$. These probabilities were derived by first fitting $K-1$ binary logit models separately to the data. The ith model included observations (no "pseudo-absences") from habitat i and K only, where $y = 1$ if individual was observed in habitat i and $y = 0$ if it was observed in the reference habitat K. From the logistic regression models, we obtained selection ratios $f_i(\boldsymbol{x})$ that models the selection between habitat i and the reference type K. Given the selection ratio $f_i(x)$ probability of selection of habitat i was estimated via the multinomial logit link:

$$\pi_i(\boldsymbol{x}) = \frac{exp(f_i(\boldsymbol{x}))}{1+\sum_{s=1}^{K-1} exp(f_s(\boldsymbol{x}))} \tag{II.1}$$

with f_i being a general functional form of the explanatory variables that was habitat-specific. f_K is 0 for identifiability reasons. The denominator of equation II.1 was the same for all i for a specific time. Explanatory variables $\boldsymbol{x}$ can be continuous or discrete, characterising the focal habitat i or properties of the individual. In particular, it can be a function of the availability of the habitat.

Habitat availability

The accurate description of the functional response requires to adequately define habitat availability and to account for its variation in time. First, we calculated the monthly

100% home range (minimum convex polygon) for each individual using the package *adehabitatHR* (Calenge, 2006). Individuals presenting biologically unrealistic home range size, due to e.g. dispersal behaviour were discarded using the 90% percentile as a cut-off value (for females: 182 ha, males: 459 ha). We used a rasterized landscape with grid cell size of $10 \times 10m^2$ to obtain the relative availability for each habitat type within the monthly home ranges.

Model components

In the model, we included the effect of time and relative availability of the habitat on habitat selection and also assessed whether there are differences in the selection behaviour between males and females. Variation in selection across individuals and years were accounted for by including random effects on the intercept for individuals (Gillies et al., 2006) and years. The availability a_i of habitat type i, i.e. the fraction of the area covered by habitat type i, varied across the home ranges of different animals j and as well as over time of year (m, month). To account for this, the logarithm of the availability $a_{jm}^{(i)}$ of a land-cover type within the corresponding monthly home range of the animal j was included as an offset term (called "base rate" in ch. 7 in Manly et al., 2002). Any deviation from such a direct proportionality with factor 1 (functional response, Mysterud and Ims, 1998) is detected by including either a linear or non-linear effect of availability. Further we investigated whether the type of functional response varied for season (growing season (Apr-Oct) and vegetative season (Nov-Mar)) and among sexes. Smoothness of the spline functions over the range of availability was controlled by setting the smoothing parameter to $\lambda = 2$ (Wood, 2006, p.128). Temporal variation in habitat selection was accounted for by including a term for time, modelled by a cyclic (tensor product) smooth function either with or without distinguishing between the sexes.

Model selection, model fit & effect size

In total we estimated 39 different models for each habitat type. In order to take into account the problem of overfitting, prediction performance of all models was measured by applying cross-validation. Model prediction performance was obtained for each habitat separately. For applying cross-validation we split the data into 5 subgroups, ensuring that a) the data of one individual is evenly spread over all ten groups and b) within the groups, data of all times of the year and the day was available.
As the prediction is a probability and the observed variable is binary, a receiver operating characteristic (ROC) curve was used (Agresti, 2002; Boyce et al., 2002). The area under

the curve (AUC) - values were calculated, averaged and used to identify the models with the highest predictive power.

We performed all analyses in the statistical software **R** (R Core Team, 2015) using the packages *mgcv* (Wood, 2006) for GAMMs and *adehabitatLT* for home range calculations (Calenge, 2006).

Results

Habitat availability and general selection

The mean monthly home range size was 70.4 ha (sd: 41.5 ha) for females and 152.8ha (sd: 101.7 ha) for males. Availability of habitats within the study area and availability within the home ranges differed noticeably for most of the habitat types (Tab. II.1).

Since home range sizes varied across months (e.g. mean for females in January: 194 ha, in June 86 ha; for males in January 306 ha, in May 461 ha), availabilities of habitat types within the monthly home ranges differed remarkably over the course of the year and partially between sexes (Supplementary material Figs. S3 and S4, i.e. young stands).

Habitat Selection Patterns

On average, roe deer selection over time varied markedly among the 11 habitat types we defined for the Bavarian forest (see Tab. II.1). In general, time-dependent variation in habitat selection differed significantly between females and males for most habitat types, except from unmanaged meadows, young stands and anthropogenic areas. The interaction of both temporal scales is observable as the pattern of circadian variations vary over the time of year, obviously driven by sunlight (see Appendix Figs. S1, S2 in Supporting Information).

In general, most habitats are selected with the same daily selection patterns throughout the year (e.g. cultivated meadows: selection during the night, avoidance during the day), which simply varies in the magnitude over the time of year (e.g. cultivated meadows: high in summer, low in winter). The variation of the magnitude of selection over the course of the year results in a seasonal alternation between high and low selection of habitats. Such a seasonal shift is observed for all habitats (Fig. S1, S2).

Functional Responses

The change in relative use of an habitat given its availability appeared to be general in the roe deer population of the Bavarian Forest National Park. We indeed found notable

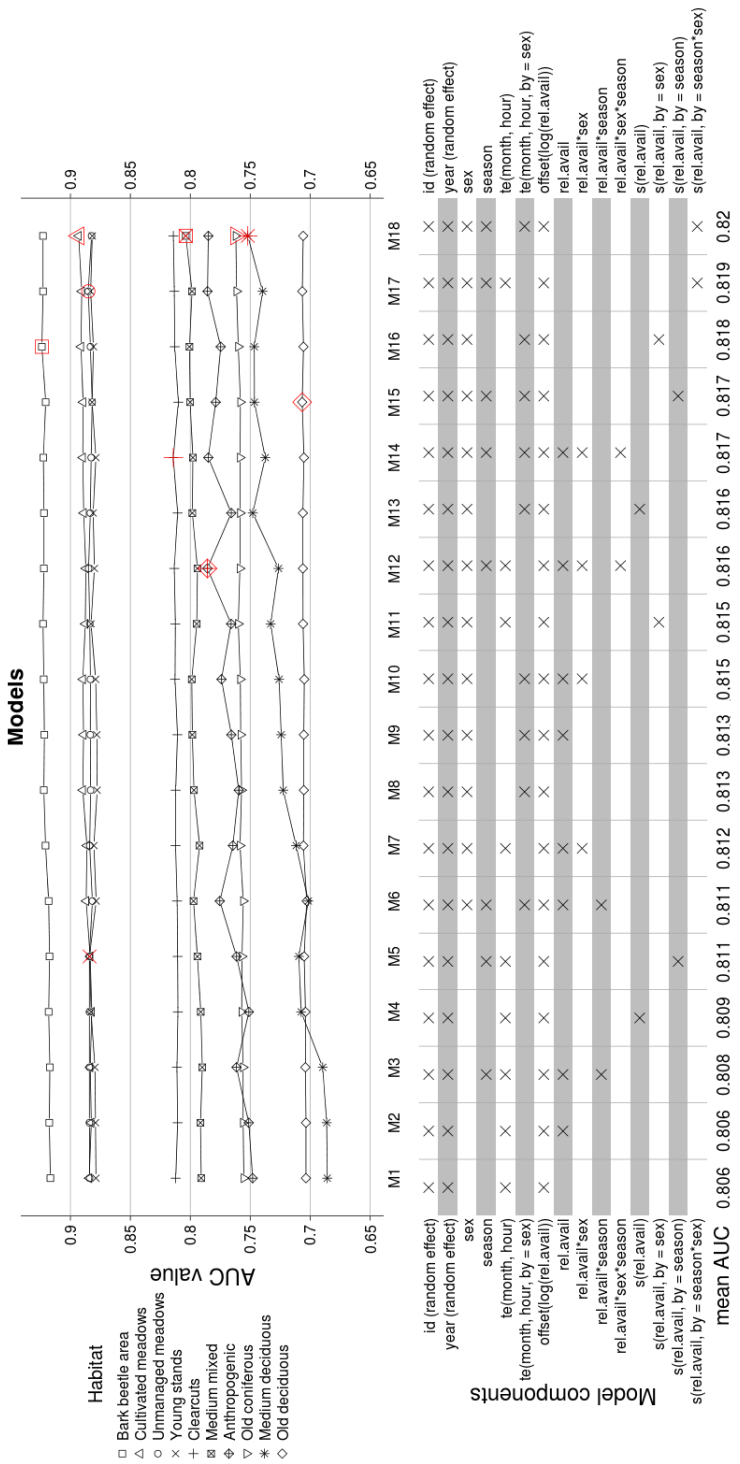
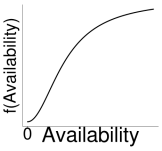
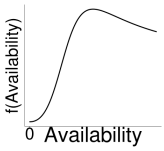


Fig. II.1 AUC values for models explaining the selection of 11 habitat types by 26 roe deer (19 males, 17 females) in the National Park Bavarian Forest, Germany from 2002 to 2011. AUC-values are in ascending order of the sum of AUC-values (over habitats). The greater the AUC value the better is the prediction performance of the model. Model components integrated in the model are shown in the table on the bottom of the figure. All models included the variable id (for individual) and year as random effects. Abbrevations: rel.avail, relative avialability of habitat type; s, smooth term, for hour and month it is a cyclic smooth function; te, cyclic tensor product smooth term; by, a replicate of the smooth is produced for each factor level of sex or season or interaction of both, respectively.

Tab. II.2 Type of functional response found for habitats in summer and winter for females and males. The form of the relation of selection probability and the relative availability of a habitat can be described by a linear response (Type I), a concave upward response (Type II) or a sigmoid response (Type III).

	Type I	Type II	Type III	Type IV
				
Summer				
	Old mixed	Cultivated meadows, Disturbance area (day), Clearcuts, Young stands, Unmanaged meadows, Medium deciduous, Old deciduous	Disturbance area (night), Old coniferous	Anthropogenic
Winter				
	Old mixed	Cultivated meadows, Clearcuts, Anthropogenic, Medium deciduous (♂), Old deciduous	Disturbance area, Young stands, Unmanaged meadows, Old coniferous	Medium deciduous (♀)

functional responses for all the 11 habitat types as estimated selection probabilities differed strongly from straight lines (Figs. II.2, S3). However, the strength of selection of old mixed stands seems to be irrelevant of its availability in the home range of the animals: Probability of selecting old mixed stands equals availability (Fig. S3).

Our analyses also revealed a distinct difference of the functional responses among habitat types, between winter and summer seasons (e.g. M5, M12, M14, M15, M17, M18 in Fig. II.1) for all except from disturbance area. In addition the shape of functional response differed between sexes to some extent (e.g. M9 vs. M10 and M13 vs. M16), except from old decidous and young stands. The use of a non-parametric smoother provided evidence for non-linear functional responses for all habitats but anthropogenic area (M12) and clearcut area (M14).

Holling 1959 described four types of patterns that relate the intake (here use) to density (here availability). When calculating the probability of use as a function of availability given the selected models (Fig. II.1) we found four main patterns (Tab. II.2): an approximately linear (type I according to Holling (1959)), a concave curve (type II), a convex curve (type III) and a decreasing curve (type IV) with increasing availability of a habitat. Generally, the strength of use, *i.e.* preference or avoidance, of a habitat at a particular time determines whether the curve is above or below the proportional use probability with use probability = availability (grey lines in Figs. II.2 and S3).

In case of a linear functional response the type of selection (high selection/avoidance) does not change with availability. We found this pattern of type I only for old mixed stands. For old mixed stands use equals availability throughout the observed range of availability (from 0.01 to 0.5). In case of a concave curve (type II) the strength of selection decreases with increasing availability. Often a switch occurs from preference to avoidance with increasing availability. In mathematical terms, the slope of this function monotonically decreases with increasing availability. We found this pattern in many habitat types (meadows, disturbance area, clearcuts, young stands (in summer), medium aged and old deciduous stands). As expected, we found type II strongly for habitats that provide primarily a single resource, *i.e.* food in case of meadows. Probability of use of cultivated meadows (Fig. II.2) by females in summer increased with increasing availability for very low values (< 0.03) with slope ≈ 10. However, for higher values of availability (> 0.1) the slope was almost 0. For many habitats, in particular in summer, the decrease of the slope resulted in a shift from preference to avoidance if the availability of a habitat exceeds a certain value.

Type III functional responses were found for old coniferous stands, young stands, unmanaged meadows and disturbance area.

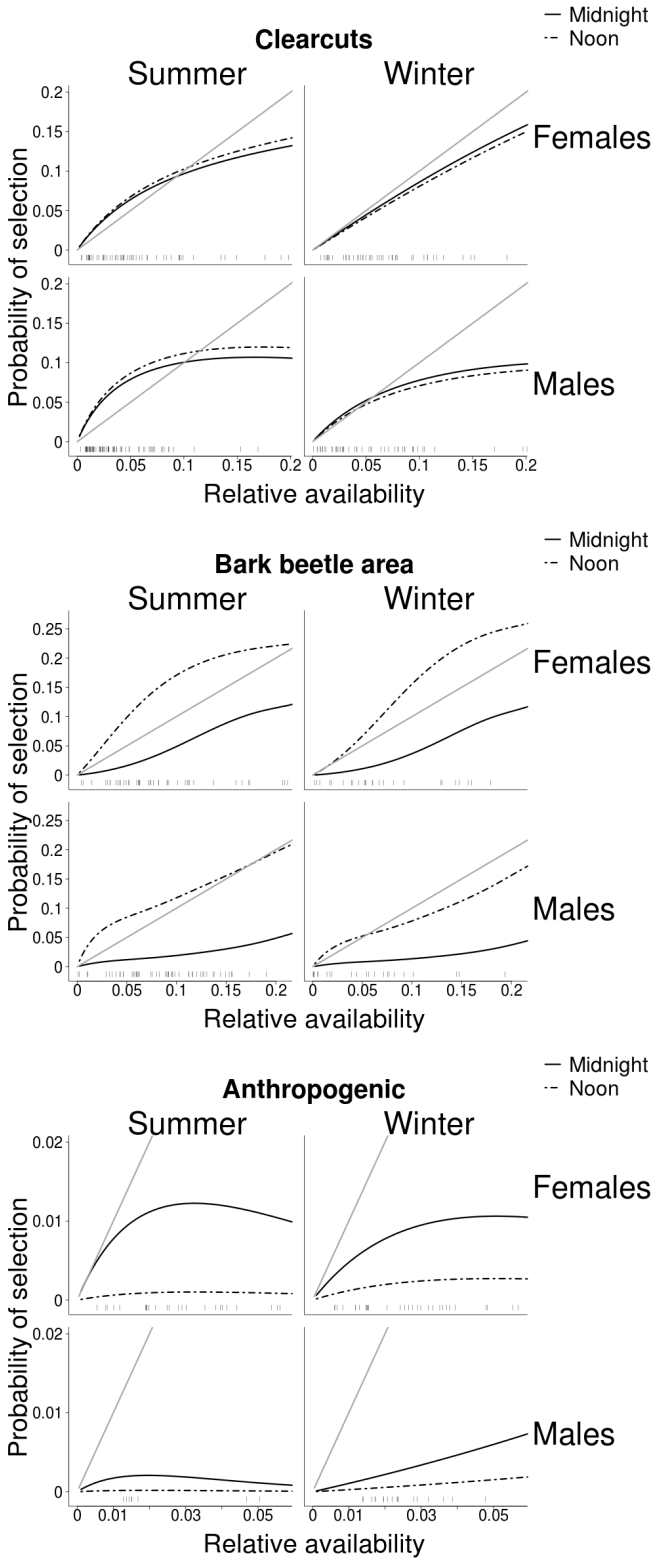


Fig. II.2 Estimated selection probability of clearcut area, disturbance area and anthropogenic area as a function of availability for summer (left column) and winter (right columns), time of day (midnight: solid line, noon: dashed line) and sex (females: top, males: bottom) by 26 roe deer (19 males, 17 females) in the National Park Bavarian Forest, Germany from 2002 to 2011. Grey lines describe a selection probability directly proportional to relative availability. Ticks above the x-axis indicate observed proportions of the habitat within the analysed monthly home ranges.

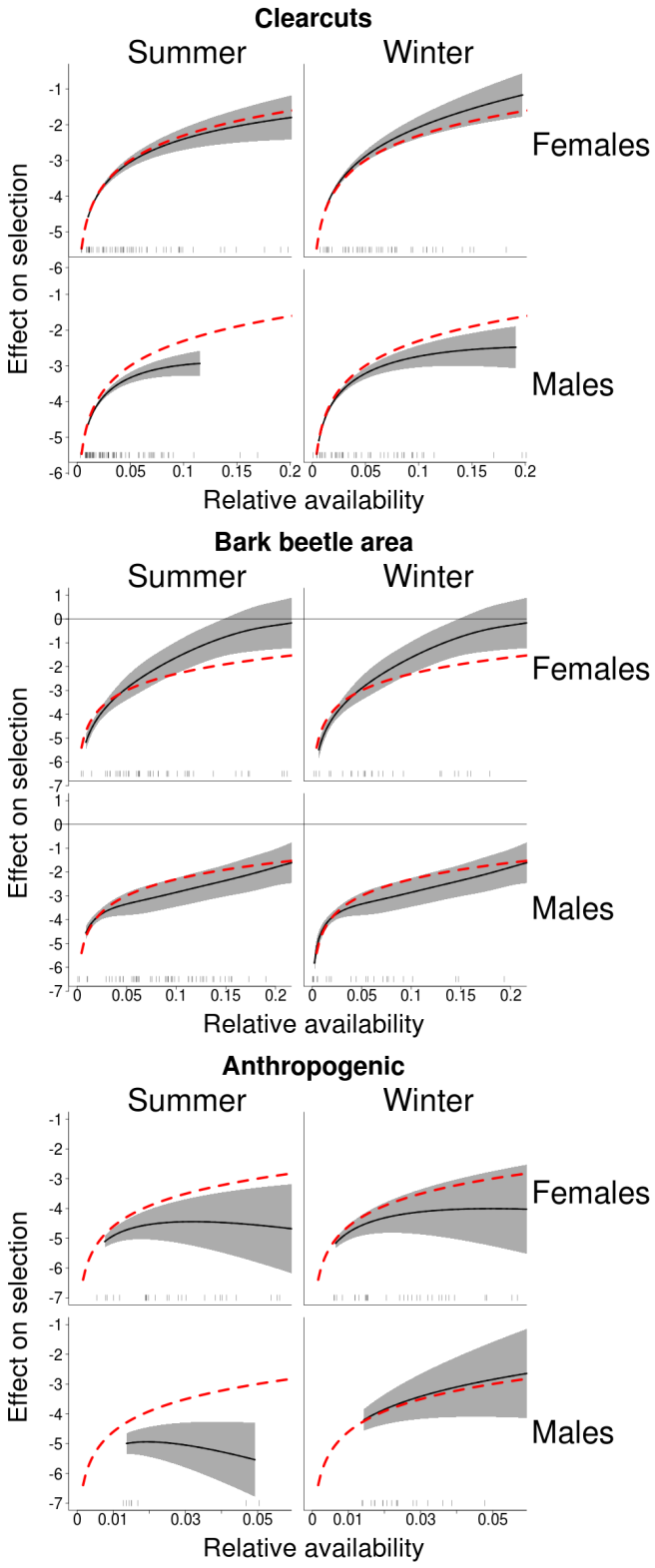


Fig. II.3 Effect of availability on strength of selection on the link scale with confidence bands for different habitats in summer and winter for 17 females and 19 males roe recorded in the National Park Bavarian Forest, Germany from 2002 to 2011. Red line indicates a proportional selection to availabilty. Ticks above the x-axis indicate observed proportions of the habitat within the analysed monthly home ranges.

Type IV was exposed in anthropogenic area (in summer) and in winter in medium deciduous stands for females only.

Functional response can also be detected on the link scale (Figs. II.3, II.4, S4). Estimated functional response differ strongly from a constant proportional increase of selection with increasing availability. However, from the shapes of the functions on the link scale, it remains difficult to determine the type of functional response. Intuitively, it is obvious that the probability of use also depends on the availability and selection strength of alternatives (Fig. S5). This is in particular true for those habitats where selection coefficients are estimated to be close to 0 (Fig. S5).

Discussion

As expected, we found pervasive evidence for functional responses in the habitat selection behaviour of roe deer, highlighting its distinct variability in shape among habitats with time and between sexes. Non-linearity in the strength of selection with habitat availability appears as a general behaviour in roe deer, occurring in almost all habitat types we considered except from the most common habitat old mixed stands. Most functional responses we describe here present a concave shape comparable to a type II according to Holling's 1959 classification. That selection strength levels off as the habitat increases in availability within the home range likely reflects the trade-offs acting on movements faced by roe deer to exploit its home range. However, we also found examples for type I, III and IV functional responses.

The Predominance of Functional Responses

On the observed ranges, we found that the relationship between use and availability of the 11 habitat types was non-linear for all seasons and, for males and females for almost all habitats (exception: old mixed stands). Functional responses were previously reported in caribou, moose and roe deer (Bjørneraas et al., 2012; Moreau et al., 2012; Samelius et al., 2013). Functional responses appear as a general behaviour in the resource selection at the home-range scale in large herbivores.

Type II functional responses are characterized by a decelerating selection strength with availability, which follows from the assumption that the consumer is limited by its capacity to process or to find food. It assumes that herbivores uses the resources for feeding. We found this type of functional response in most habitat types, especially in summer.

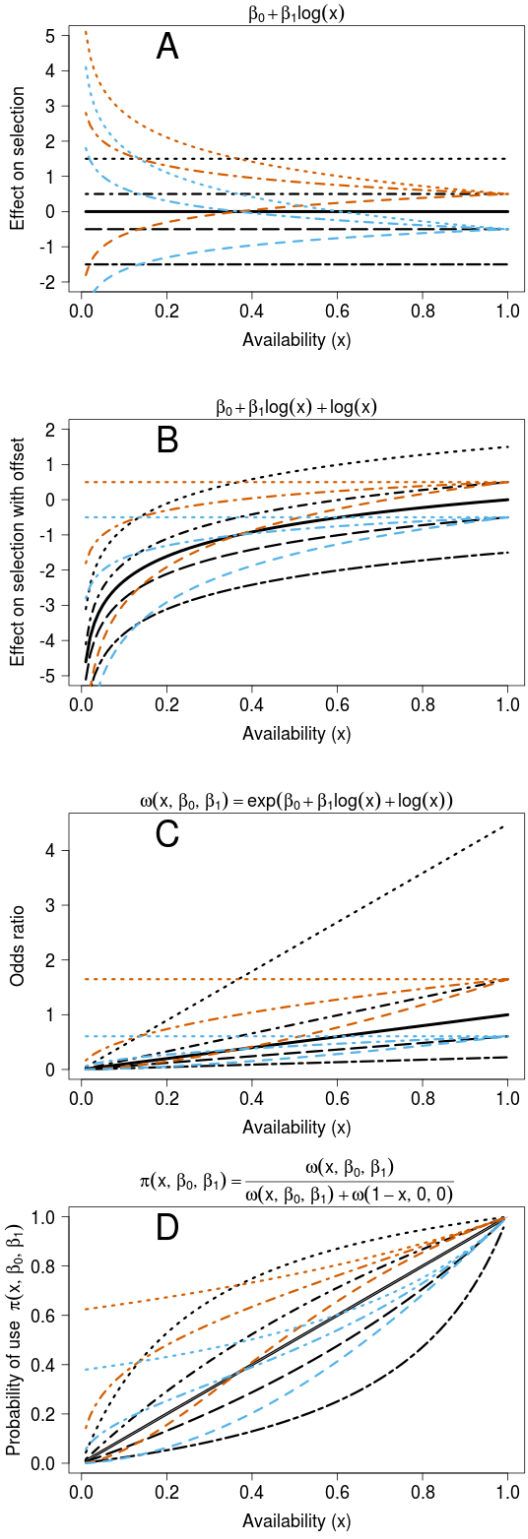
In carnivores Holling type III functional responses emerge as a result of a learning process or of a prey switching by predators (Real, 1977). Selection is slow at low availabilities but then increases more rapidly than a proportional selection. Type III functional responses were found for the disturbance area, in winter only for females at day and night, for males only at night. As the shape of the functional response is not particularly distinct as for type II, we remain careful with the interpretation. Old coniferous are mostly avoided by roe deer over its full range of availability. However, if availability exceeds some threshold (≈ 0.2), selection increases, resulting in a type III of functional response.

Type IV (dome-shaped) functional response has been found in several predator-prey systems (see Líznarová and Pekár, 2013, for an overview). The reason that predator consumption decreased with increasing prey density are various, e.g. confusion of the predator (Jeschke and Tollrian, 2007), toxicity of the prey (Claver et al., 2003) or limitation of the predator's mobility (Heuermann et al., 2011). In habitat selection, an increase of availability seems to have negative effects on the animals, that avoidance of this habitat increase with availability as we have found for anthropogenic area. These areas likely provide highly nutritional forage, but at the same time itposes an higher risk with the consequence of an increased investment in allertness to avoid encounters with humans (Benhaiem et al., 2008; Shannon et al., 2014). The tendency to balance between food and human disturbance seems to decrease with increasing availability of anthropogenic area in the home range of roe deer.

What shapes the Functional Response for Herbivores?

From the model point of view, there is no functional response if the use of a habitat equals its availability, *i.e.* for *proportional use*.

However, if a habitat is favourably selected over others, functional response is the result, as relative use is greater than relative availability. If a habitat is favoured throughout the whole range of its theoretical availability ranging from 0 to 1, the use curve will be above the proportional use line. But nonetheless saturation will occur. Saturation in use with increasing availability will occur due to the natural restrictions as relative use is limited by 1 (Fig. II.4). In practice it means, an animal can not spend more time in a habitat than there is time available. Such a saturation curve for one habitat has direct implications for the other available habitats as the total amount of time has to be allocated among all available habitats (Fig. S5). If one habitat is favourably selected over all the others, the use curve of all other habitats will be below the proportional use line.



β_0	β_1	Lty	Hty
0	0	—	I
1.5	0	····	II
0.5	0	-·-	II
-0.5	0	— -	
-1.5	0	— ·	
0.5	0.5	– –	III
0.5	-0.5	-·-	II
0.5	-1	····	
-0.5	0.5	– –	
-0.5	-0.5	-·-	II
-0.5	-1	····	

Fig. II.4 Concept plots of functional response for different values of β_0 and β_1 in different representations, β_0 determines the overall selection and β_1 models the effect of availability on selection: effect of availability on selection without (A) and with an offset for availability (B), effect of availability on the odds ratio (C), given that $\omega(x, \beta_0, \beta_1) = 1$ of the reference category; and the effect of availability on use given a simple multinomial/binomial model. Only in D functional response in habitat selection can be directly referred to Holling's (1959) types (Hty). However, this is a very simplified model for use with only two habitats, where the selection of the second alternative does not vary with availability. The effect of a varying availability on selection of the alternative is shown in Fig. S5 in the supplementary material. R-Code is provided in S6.

Fig. II.4

The example of an at all times favoured habitat is unlikely for herbivores in nature as these have needs that vary in time and, in addition, conditions vary in time (Hebblewhite and Merrill, 2009; Bjørneraas et al., 2011). Moreover, habitat selection of herbivores is characterised by a trade-off between competing resources, *e.g.* food and cover. For roe deer, using meadows statisfies energy demands and at the same time poses a higher risk of disturbances (*e.g.* caused by humans, Frid and Dill, 2002). Contrary, in old forest stands herbivores may find shelter but lower quality forage (Bjørneraas et al., 2012). Hence, roe deer must balance between the opposing conditions which results in a functional response in habitat selection (Mysterud and Ims, 1998). For roe deer we found patterns of curves that show saturation for relatively small values for relative use. For example for females in summer during the day the use of cultivated meadows (Fig. S3) is very high (≈ 0.2) for low availabilities (≈ 0.05) and does rarely increase with further increasing availability. This means that the animal does not need to spend more time on a meadow than one fifth of its time. Certainly, spending a particular amount of time on meadows satisfies the needs of roe deer, which does not change if availability increases within the home range. However, if availability is greater than this necessary amount of time, selective use will switch to avoidance. This is because, herbivores have also the urge to hide from disturbances, resulting in a trade-off between food and cover (Godvik et al., 2009). This pattern is found for almost all habitats of type II (and III) which implies that an animal determines its site selection mainly by its internal needs and to a lesser extent by the availability of habitats, given the already fixed composition of available habitats.

The composition of available habitats is determined by the roe deer in an earlier step by selecting the home range on a larger scale. The heterogenuous composition of the home range is necessary to choose between different options at different times. We have shown that selection for habitats differs between seasons and times of day and so do the curves for functional response. Different shapes of the curve for functional response for different times of day and seasons support the finding that primarily the needs of the animals and to a much lesser extent the availability of a habitat determines the use of a habitat. Habitat are not selected per se but are selected for what they provide to animals.

However, availability may influence habitat selection for those habitats where functional response of type III was found. This type may occur if an animal needs to become accustomed to a habitat type. An animal can avoid unsuitable conditions of a habitat if it is rare within its home range, but have to opportunistically use it if it exceeds some threshold. In this case availability more strongly influences the use of a habitat. Another explanation can be that animals need some amount of energetic costs to enter those habi-

tats, and raising this costs must be balanced by a reasonable benefit such as coming from sufficient availability. For example we have found type III in disturbance areas where there are fallen trees jammed all around which probably hamper the mobility of roe deer. In particular in winter, snow layers over hollows poses a righ risk for roe deer te become cooped up. However, high energetic forage from young regeneration may compensate the high effort to reach this area. Hence, availability influences habitat selection.

Also for habitats with functional response of type IV, availability determines its use, as we found for anthropogenic area (Fig. II.2). Here, an increase of availability seems to have negative effects on the animals, that avoidance of this habitat increase with availability. In a prey-predator-sytem, functional response of type IV is assumed to take place due to resource toxicity or predator confusion (Gentleman et al., 2003). Disturbances by humans may function likewise.

Generalist vs. Specialist

As roe deer is specialized on using specific habitats to fulfill its needs we detected these distinct functional curve patterns. As the needs and the conditions in habitats vary for different times (day/night, seasons), shapes of the curves differ for different times and hence types of functional response can also differ for the very same habitat for different times (e.g. disturbance area, Fig. II.2). For those habitats that offer a low variety of resources, such as mere forage on meadows, we found a strong saturation that occurs already for low values of availability. Here, the roe deer is focused or specialized on forage intake and one would expect such saturation curve (Holling, 1959). This finding agrees with the foraging strategie of herbivores, which first fill their stomachs and rest afterwards in a safer place to chew and ruminate (Kamler et al., 2007). However, those habitats that provide both food and cover such as young stands show only a slight attenuation with increasing availability. In such habitats, roe deer is not focused on a single resource and acts as a generalist.

Type II with a continuous decrease of selection with habitat availability is the most commonly observed curve, especially in summer (Fig. II.2). However, the degree of saturation differs between habitats, seasons and daytime. In habitats that are mainly used for foraging, time spent in these habitats should be strongly positively correlated with forage intake. We therefore argue that for grazers the saturation should be more pronounced in habitats that are used for foraging only and which are characterized by a simple structure due to the strong correlation between bite size and intake of biomass (see Gross et al., 1993). For roe deer as a browser, bite size depends on the leaf size

(Gross et al., 1993), and hence, there is not necessarily a linear relationship between time spend in a habitat and biomass intake. Consequently, the time needed to fill the stomach depends on the detection rate of suitable forage that strongly varies between habitats. In habitats where suitable forage is abundant and time of detection is low, such as on meadows and clearcuts, use of a habitat should also be directly related to forage intake as for grazers. Hence, functional response of type II should be predominant in habitats mainly used for the purpose of foraging.

Accounting for Functional Responses in Habitat Selection Studies

Holling (1959) based his models about functional response on laboratory experiments where a predator was faced with a single resource. However, we analyse field data, where animals are confronted with multiple resources. We use multinomial models that take into account the multinomial structure of the data, *i.e.* the animals can choose between different habitat types. In our models, we relate probability of use to the availability of a habitat. This relation is subjected to some straightforward model restrictions: if availability is zero, probability of use is also zero, and if availability is one, probability of use is also one (Fig. II.4). In between these extremes, the shape of the curve is determined by *i)* the type of general selection (selective use/avoidance), *ii)* the type of functional response, but also *iii)* the composition of the home range, meaning the suite of alternatives an animal can choose from (Fig. S5). This, however, can not be tested in a laboratory and this is a great challenge when analysing functional response in the field. The bumps in the curves for functional response of some habitats (e.g. medium mixed in Fig. S3) may be due to different compositions of habitats in the home range of the different animals. For instance, for medium mixed, old coniferous and old deciduous one would expect rather straight lines for increasing availabilities. These wave-like curves may arise when in some home ranges similar habitats also occurs in the home range to a great extent, then saturation takes earlier place, and in other home ranges this habitat with its characteristics is not accompanied by similar ones, then saturation in selection takes place for higher availabilities. The composition is not accounted for in our models as it would substantially increase the model complexity.

The ability to explore the shape of functional responses in habitat selection using multinomial logit models comes at the costs of describing the landscape with discrete categorical variables. As compared to the generally used RSF (Manly et al., 2002), the multinomial logit model accounts explicitly for variation in resource availability for animals, be it in time or among individuals. We detected a non-linear functional responses

for almost all habitat types. Assuming a linear relation between use and availability of a habitat *a priori* as in RSF is not supported for roe deer, except from the most common habitat type old mixed stands. The gain in predictive power of our model with and without non-linear relation is, however, slight (Fig. II.1) and we can assume that results obtained from a RSF would not be strongly biased. Hence, using spline functions for modelling functional response in habitat selection is not particularly necessary (M14 vs. M18 in Fig. II.1). In particular, for larger availabilities predictions might follow a more distinct and biologically interpretable pattern then estimated by spline functions. However, the "wiggliness" might also be due to a relatively low sample size for some habitat types (e.g. medium mixed) and the earlier mentioned heterogeneity in habitat composition. But we do see an advantage to favour splines over linear effects. Simple linear effects are not capable to model functional response for very low values that exceed a constant selection (see e.g. old deciduous or cultivated meadows). We advise to use a combination of splines and linear effects. However, we realise that linear effects would be easier to gain biologically relevant insights.

Conclusion

Functional response in the use of habitats is a common pattern found for roe deer as a large herbivore in the Bavarian Forest National Park, Germany. The use of habitats is primarily driven by the internal needs of the animals if the range of resources is narrow. The use of a habitat is determined more strongly by its availability if the habitat offers a large range of resources or opposing resources (*e.g.* food and cover). Time-varying shapes of functional response reveal the trade-off between cover and food in the habitat selection of roe deer. Multinomial logit models are highly suitable for modelling functional response in habitat selection. With such models use and availability of habitats can be related while accounting for the fact that animals can choose between multiple habitats.

Acknowledgements

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Supporting Information – Appendix

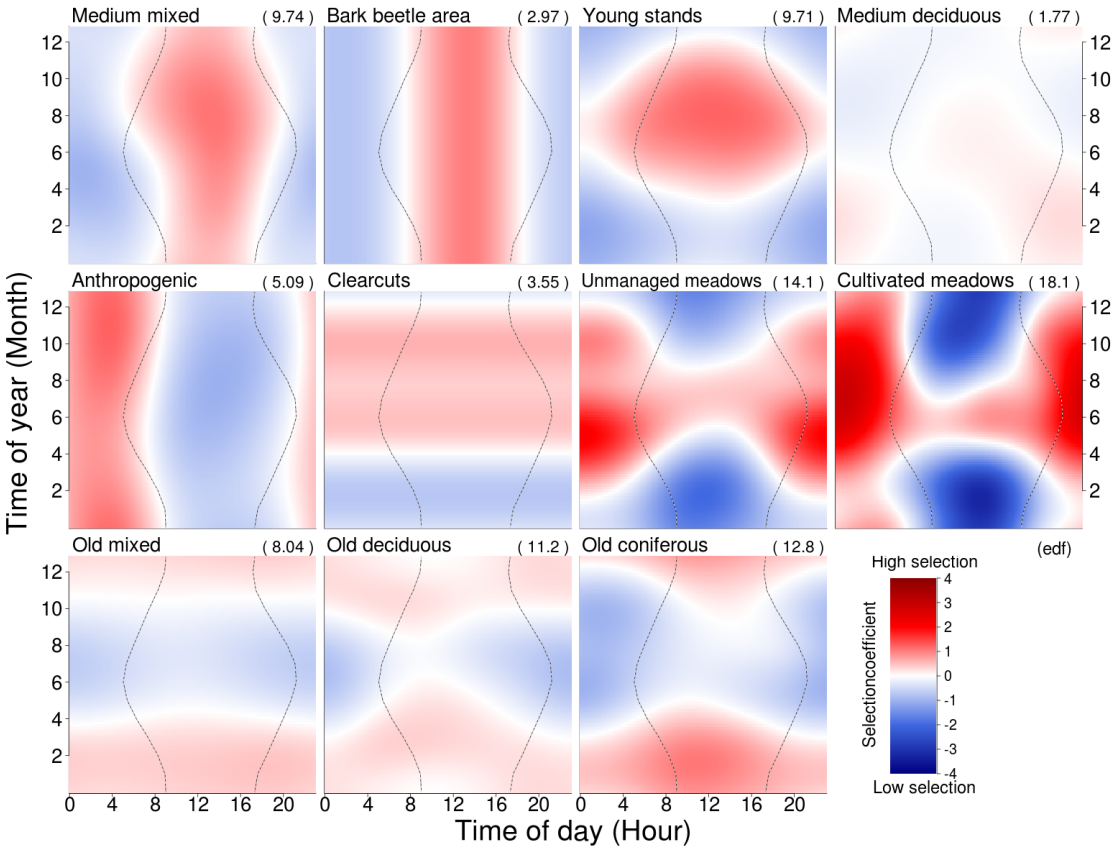

Fig. II.S1 Habitat selection on 3rd order (within home range): Variation of the selection coefficient over time of year (y-axis) and day (x-axis) for 17 **female** roe deer in the Bavarian Forest National Park, Germany recorded from 2002 to 2011. Colour indicates the value of the selection coefficient for the respective land-cover type. Estimated degrees of freedom (edf) refers to the "wiggliness" of the smooth.

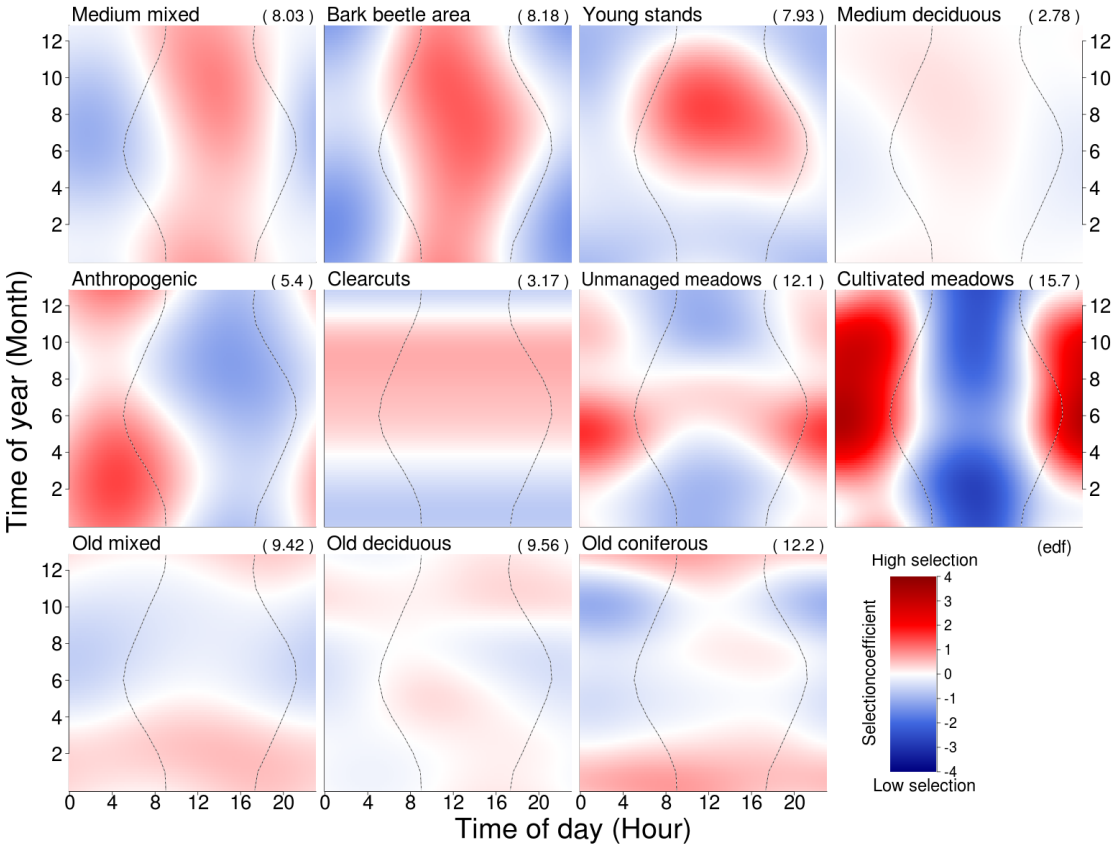

Fig. II.S2 Habitat selection on 3rd order (within home range): Variation of the selection coefficient over time of year (y-axis) and day (x-axis) for 19 **male** roe deer in the Bavarian Forest National Park, Germany recorded from 2002 to 2011. Colour indicates the value of the selection coefficient for the respective land-cover type. Estimated degrees of freedom (edf) refers to the "wiggliness" of the smooth.

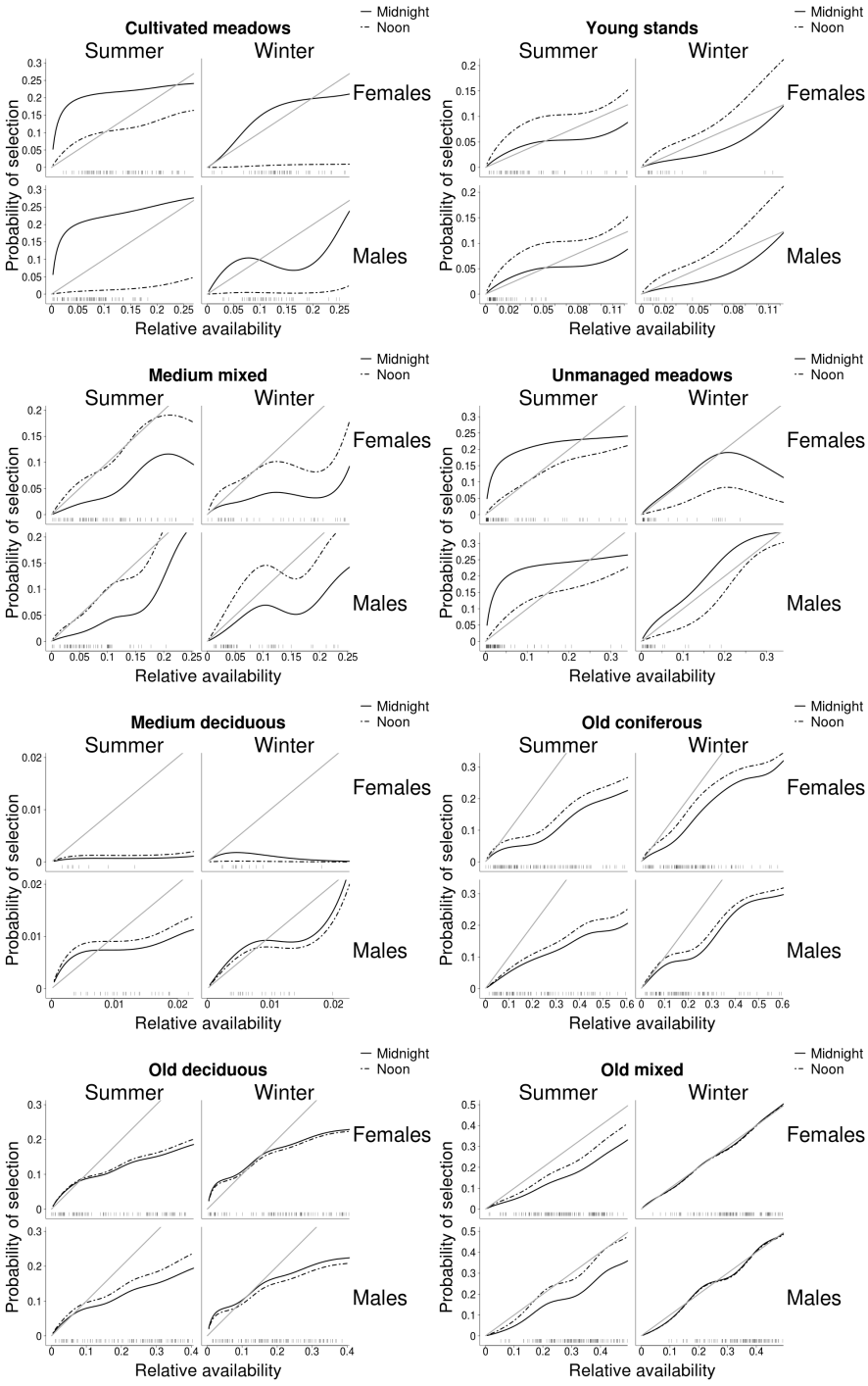

Fig. II.S3 Shapes of functional response for different habitats in summer and winter for 17 females and 19 males roe deer during night (solid line) and day (dashed line) recorded in the National Park Bavarian Forest, Germany from 2002 to 2011. Grey line indicate proportionality of probability to availabilty. Strokes above the x-axis indicate observed proportions of the habitat within the analysed monthly home ranges.

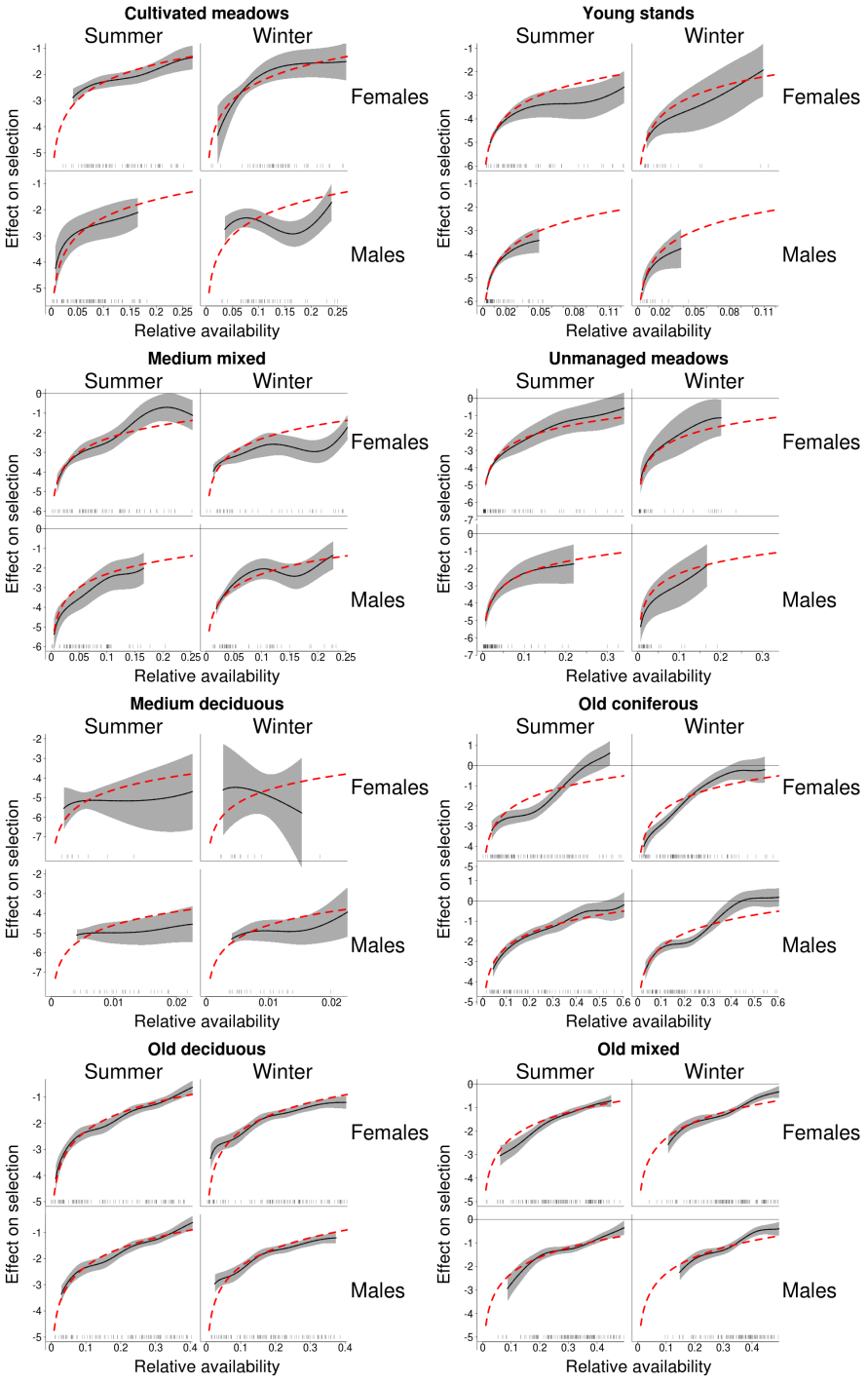

Fig. II.S4 Effect of availability on strength of selection on the link scale with confidence bands for different habitats in summer and winter for 17 females and 19 males roe recorded in the National Park Bavarian Forest, Germany from 2002 to 2011. Red line indicate a proportional selection to availabilty. Strokes above the x-axis indicate observed proportions of the habitat within the analysed monthly home ranges.

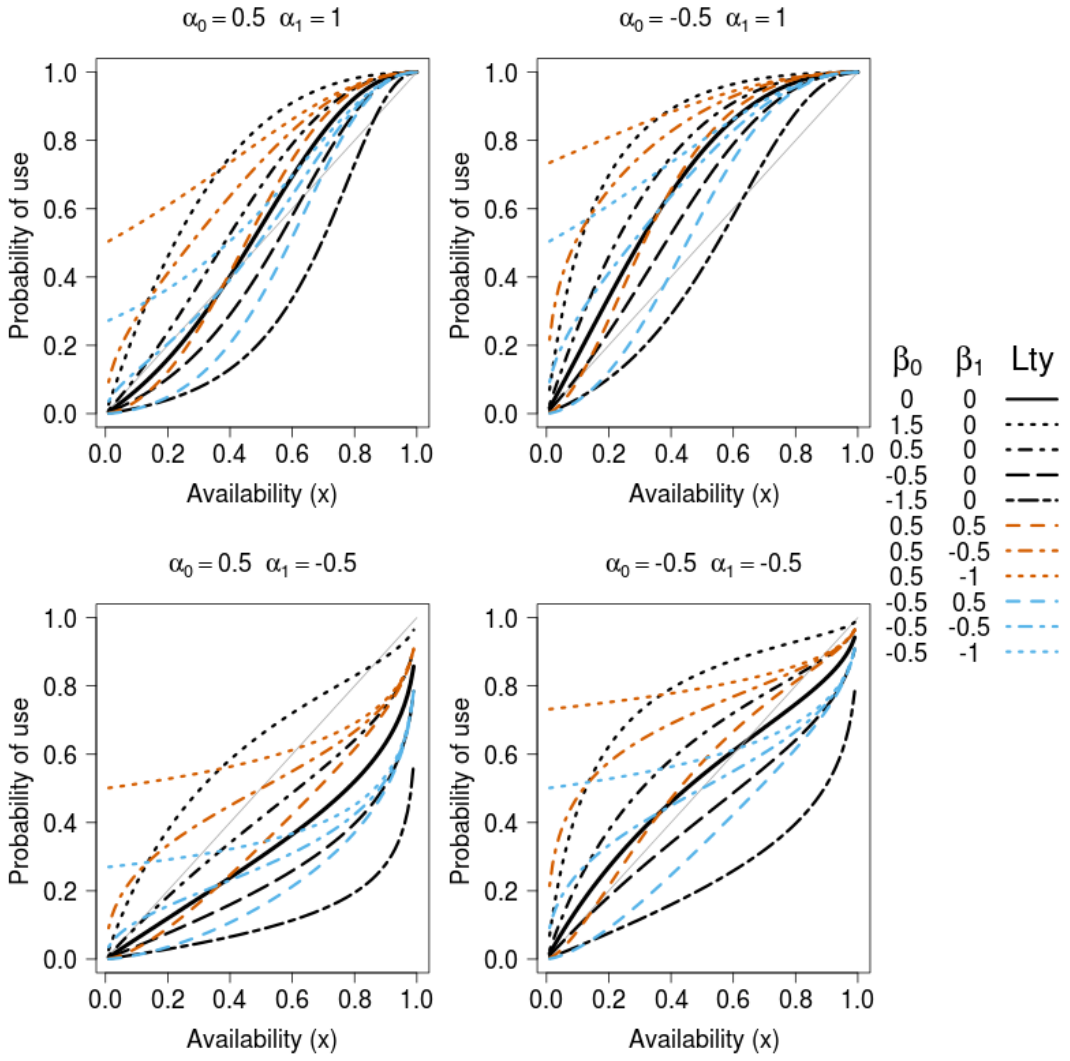

Fig. II.S5 Effect of a varying availability of the two alternatives on use, where probability of use is $\pi(x, \beta_0, \beta_1, \alpha_0, \alpha_1) = \frac{exp(\beta_0+\beta_1 x)}{exp(\beta_0+\beta_1 x)+exp(\alpha_0+\alpha_1 x)}$. The Holling type varies also for different values of α_0 and α_1, which shows that not only the parameter of selection determines the Holling type but also the parameter of selection of the alternatives. R-Code is provided in S6.

Appendix S6 R-Code. R-Code that visualizes the effect of parameters on selection, odds ratios and probability of use (see Fig. S5).

```
# Author: Dupke
#     ##############################################################################


x <- seq(0.01,1,length=100)

#effect of x on selection with offset
sel_w <- function(beta0, beta1,x){
         beta0+beta1*log(x)
}

#effect of x on selection with offset
sel <- function(beta0, beta1,x){
         sel_w(beta0, beta1,x)+log(x)
}

# odds ratio
OR<- function(beta0, beta1,x){
         exp(sel(beta0, beta1,x))
}
OR2<- function(beta0, beta1,x){
                 exp(beta0)*x^(beta1+1)
}
# multinomial logit link function
getProb <- function(beta0, alpha0,beta1,alpha1,x){
         OR(beta0,beta1,x)/(OR(beta0,beta1,x)+OR(alpha0,alpha1,(1-x)))
}

# define parameters
#########
# use = availability
B0 <- 0
# use >> availability
B0_1 <- 1.5
# use > availability
B0_2 <- 0.5

# use < availability
B0_3 <- -0.5
# use << availability
B0_4 <- -1.5

##use > availability, selection coefficient increases slowly with
    availability
B1_0 <- 0.5
B1_1 <- 0.5
##use > availability, selection coefficient decreases with availability
```

```
B2_0 <- 0.5
B2_1 <- -0.5

##use > availability, selection coefficient decreases with availability
B3_0 <- 0.5
B3_1 <- -1
## use < availability selection coefficient increases  with availability
B4_0 <- -0.5
B4_1 <-  0.5

##use < availability, selection coefficient decreases slowly with
    availability
B5_0 <- -0.5
B5_1 <- -0.5

##use < availability, selection coefficient decreases with availability
B6_0 <- -0.5
B6_1 <- -1

#graphics
col1 <- 1
col2 <- 2#"#D55E00"
col3 <- 3#"#56B4E9"
col4 <- 4#"#009E73"

lwd1 <- 4
lwd2 <- 3
cxm <- 1.5
cxA <- 3

#make table
DF <- data.frame(matrix(c(B0,0,B0_1,0,B0_2,0,
B0_3,0,B0_4,0,B1_0,B1_1,B2_0,B2_1,B3_0,B3_1,B4_0,B4_1,B5_0,B5_1,B6_0,B6_1),
    ncol=2,
byrow=TRUE, dimnames=list(c(),c("beta0","beta1"))),
col=c(rep(col1,5),rep(col2,3),rep(col4,3)),
lty=c(1:5,2:4,2:4),
lwd=c(1,rep(lwd2,10)))

#par(mfrow=c(2,2),las=1,cex=1,mar=c(5,5,4,0.5))
layout.show(layout((matrix(c(1:4,rep(5,4)),ncol=2)),widths=c(2.1,1)))
par(las=1,cex=1,mar=c(5,5,4,0.5))

plot(x,sel_w(B0,0,x),type="l",ylim=c(-2,5), ylab  = "Effect on selection",
    xlab = "Availability (x)",col=col1,cex.axis=1.5,cex.lab=1.5,lwd=lwd1)
for(i in 2:nrow(DF)) lines(x,sel_w(DF[i,"beta0"],DF[i,"beta1"],x),col=DF[i,"
    col"],lty=DF[i,"lty"],lwd=DF[i,"lwd"])
mtext(expression(beta[0]+beta[1]*log(x)),cex=cxm)
mtext("A",adj=0.2,line=-2.5,cex=cxA)

################
```

```
#selection with offset (log(availability))
plot(x,sel(B0,0,x),type="l",ylim=c(-5,2), ylab  = "Effect on selection with offset", xlab = "Availability (x)",col=col1,cex.axis=1.5,cex.lab=1.5,lwd=lwd1)
for(i in 2:nrow(DF)) lines(x,sel(DF[i,"beta0"],DF[i,"beta1"],x),col=DF[i,"col"],lty=DF[i,"lty"],lwd=DF[i,"lwd"])

mtext(expression(S=beta[0]+beta[1]*log(x)+log(x)),cex=cxm)
mtext("B",adj=0.2,line=-2.5,cex=cxA)

########################
# Odds ratios
plot(x,(OR(B0, 0,x)),type="l",ylim=c(0,4.5), ylab  = "Odds ratio", xlab = "Availability (x)",col=col1,cex.axis=1.5,cex.lab=1.5,lwd=lwd1)
for(i in 2:nrow(DF)) lines(x,OR(DF[i,"beta0"],DF[i,"beta1"],x),col=DF[i,"col"],lty=DF[i,"lty"],lwd=DF[i,"lwd"])
mtext(expression(paste(omega(x,beta[0],beta[1])==exp(beta[0]+beta[1]*log(x)+log(x)))),cex=cxm)
mtext("C",adj=0.2,line=-2.5,cex=cxA)

####################
# Use
plot(x,getProb(B0,B0,0,0,x),type="l",ylim=c(0,1), ylab  = expression(paste("Probability of use  ",pi(x,beta[0],beta[1]),"")), xlab = "Availability (x)",col=col1,cex.axis=1.5,cex.lab=1.5,lwd=lwd1)
lines(x,x, col="darkgrey")
for(i in 2:nrow(DF)) lines(x,getProb(DF[i,"beta0"],0,DF[i,"beta1"],0,x),col=DF[i,"col"],lty=DF[i,"lty"],lwd=DF[i,"lwd"])

mtext(expression(paste(pi(x,beta[0],beta[1])==frac(omega(x,beta[0],beta[1]),omega(x,beta[0],beta[1])+omega(1-x,0,0)))),cex=cxm)
mtext("D",adj=0.2,line=-2.5,cex=cxA)

#
    ##############################################################################


## make overview table

par(mar=c(0,1,0,1))
plotentry <- function(beta0,beta1,y,coli,ltyi,Hty,cex=1.5,...){
        text(2,y,beta0,cex=cex,...)
        text(6,y,beta1,cex=cex,...)
        lines(list(9,11),list(y,y),col=coli,lty=ltyi,lwd=3)
        text(14,y,Hty,cex=cex,...)
}

plot(0,0,type="n",xlim=c(0.5,16),ylim=c(-10,30),bty="n",xaxt="n",yaxt="n",xlab="",ylab="")
j <- 6
for(i in nrow(DF):1) {
        plotentry(DF[i,"beta0"],DF[i,"beta1"],j,coli=DF[i,"col"],ltyi=DF[i,"
```

```
            lty"],Hty="")
131         j <- j+1
132 }
133 plotentry(expression(beta[0]),expression(beta[1]),Hty="Hty",j+1,1,ltyi=0,cex
        =2)
134 text(10,j+1,"Lty",cex=2)
135 #text(14,i+10.5,"Hty",cex=2)
136
137 abline(h=j+0.5)
138
139 ##############################################
140 # use for different alphas
141 # Use
142
143 #par(mfrow=c(2,2),las=1,cex=1,mar=c(5,5,4,0.5))
144 layout.show(layout((matrix(c(1:4,5,5),ncol=3,byrow=FALSE)),widths=c
        (2.1,2.1,1)))
145 par(las=1,cex=1,mar=c(5,5,4,0.5))
146
147 for(alpha0 in c(0.5,-0.5)){
148         for(alpha1 in c(1,-.5)){
149 plot(x,getProb(B0,alpha0,0,alpha1,x),type="l",ylim=c(0,1), ylab  =
        expression(paste("Probability of use ")), xlab = "Availability (x)",col=
        col1,cex.axis=1.5,cex.lab=1.5,lwd=lwd1,
150                 main=substitute(paste(alpha[0]==a0,"  ",alpha[1]==a1),list(
                        a0=alpha0,a1=alpha1)),cex.main=cxm)
151 lines(x,x, col="darkgrey")
152 for(i in 2:nrow(DF)) lines(x,getProb(DF[i,"beta0"],0,DF[i,"beta1"],0,x),col=
        DF[i,"col"],lty=DF[i,"lty"],lwd=DF[i,"lwd"])}
153 }
154
155 par(mar=c(0,0,0,0))
156 plotentry <- function(beta0,beta1,y,coli,ltyi,cex=1.5,...){
157                 text(2,y,beta0,cex=cex,...)
158                 text(7,y,beta1,cex=cex,...)
159                 lines(list(10,14),list(y,y),col=coli,lty=ltyi,lwd=3)
160 }
161
162 plot(0,0,type="n",xlim=c(0.5,16),ylim=c(-10,30),bty="n",xaxt="n",yaxt="n",
        xlab="",ylab="")
163 j <- 6
164 for(i in nrow(DF):1) {
165         plotentry(DF[i,"beta0"],DF[i,"beta1"],j,coli=DF[i,"col"],ltyi=DF[i,"
            lty"])
166         j <- j+1
167 }
168
169 plotentry(expression(beta[0]),expression(beta[1]),j+1,1,ltyi=0,cex=2)
170 text(12,j+1,"Lty",cex=2)
```

Research paper III

Claudia Dupke, Christophe Bonenfant, Marco Heurich, Björn Reineking

Quantifcation of repeatability in habitat selection behaviour

Summary: Based on a novel framework, quantification of repeatability in habitat selection is quantified and reveals a potential for natural selection acting on habitat selection behaviour for red deer.

Authors affiliation:

Claudia Dupke*[1], Christophe Bonenfant[2] Marco Heurich[3,4], Björn Reineking[1,5],

[1] Biogeographical Modelling, Bayreuth Center of Ecology and Environmental Research BayCEER, University of Bayreuth, Universitätsstr. 30, 95440 Bayreuth, Germany

[2] Université de Lyon, F-69000, Lyon, Université Lyon 1, CNRS, UMR5558, Laboratoire de Biométrie et Biologie Évolutive, F-69622, Villeurbanne, France

[3] Chair of Wildlife Ecology and Management, University of Freiburg, Tennenbacher Str. 4, 79106 Freiburg, Germany

[4] Department of Research and Documentation, Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany

[5] Université Grenoble Alpes, Irstea, UR EMGR 2 rue de la Papeterie BP 76, 38402 St-Martin-d'Héres, France

* corresponding author

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Summary

1. The value of repeatability is widely used to quantify the consistency of animal behaviour at the individual level. In the context of movement ecology, movement trajectories are particularly well suited as these provide repeated samplings of discrete habitat choice of individuals. Even though repeatability in habitat selection of animals would have direct implications for conservation and evolution theory, there is a lack of such studies which might be due to methodological obstacles.
2. Mixed effects models have become the gold standard in calculating repeatability, and we here extend the class of covered models to mixed conditional logistic regression, which is commonly used in step selection function (SSF) analyses. Using a latent variable formulation of the SSF model we derive the quantification of repeatability in habitat selection behaviour of animals. We show that it is biologically meaningful that repeatability of habitat selection explicitly depends on environmental conditions. We use Bayesian statistics to estimate site selection of animals with respect to an environmental covariate that accounts for variation among and within individuals in environmental preferences. Based on these estimates, we calculated the value of repeatability for habitat selection behaviour and provide associated uncertainty estimates.
3. We evaluate the method using computer simulations, and apply it to quantify variability in habitat selection behaviour of male and female red deer (*Cervus elaphus*) at three different times of day in the Bavarian Forest National Park, Germany, based on GPS relocation data. We found considerably different posterior distributions for selection of forest cover on the population level between day and night between both males and females. However, only for females we found differences in repeatability during the day, with higher repeatability of selection for cover during the day, a pattern that was driven by the relatively high variation in selection among females during the day.
4. Given ongoing changes in habitat conditions, the ability of species to adapt to changing environmental conditions assumes increasing relevance. Repeatability of habitat selection can provide important information about persistent variation in how individuals respond to the environment, and thereby contribute to an improved understanding about animal movement useful for wildlife management.

Introduction

Phenotypic variability among individuals is a central tenet of evolutionary theory (Darwin, 1859) as it reflects the opportunity for selection (Crow, 1958; Arnold and Wade, 1984). For instance, in the current context of global changes, phenotypic variability among individuals could allow species to cope with new and rapidly changing environmental conditions (Sih et al., 2012). For motile animals, fitness is related to resource selection (Gaillard et al., 2010). The degree of plasticity in movement behaviour refers to the ability of animals to adapt habitat selection to environmental changes such as deterioration of local conditions or habitat loss on broader scales (Cagnacci et al., 2011). Consequently, the behavioural variability in the context of habitat selection is of primary interest for conservation (Jeltsch et al., 2013). The question arises whether and to what extent are animals able to adjust their behaviour to changing quality and distribution of habitats. For example, it has recently been shown for whooping cranes (*Grus americana*) that experienced individuals are important in innovating migration patterns and thus in adapting to changing climatic conditions (Teitelbaum et al., 2016).

Investigation of the structuring factors of individual difference in habitat selection behaviour showed that fixed attributes like sex (Marchand et al., 2015), or varying attributes like age (Nielson et al., 2002) could account for part of the observed variability. Habitat selection behaviour is also eminently context-dependent and may vary in time and space for a given individual (Godvik et al., 2009; Dupke et al., 2016). However, in the context of evolution, phenotypic variability per se is insufficient for characterising the role of natural selection on behavioural traits (Dingemanse and Réale, 2005). Natural selection can only operate on animal behavioural traits that sufficiently and repeatedly differ between individuals (Boake, 1989). The extent to which a phenotypic trait is consistently expressed by a given individual is measured by its repeatability (R), which under certain conditions can be interpreted to set an upper bound for the heritability of a trait (Dohm, 2002).

Repeatability is generally estimated empirically from observational data as the fraction of the observed differences in behaviour that is due to variation among individuals by a variance partitioning of a quantitative trait into between- and within-individual variance components (Dingemanse et al., 2010; Plard et al., 2012):

$$R = \frac{\sigma_v}{\sigma_v + \sigma_w} \tag{III.1}$$

where σ_v is the variation among individuals and σ_w is the within-individual variance.

The value of repeatability is widely used to quantify the consistency of individual differences in animal behaviour (Bell et al., 2009) and can be used as test and a quantification of personality (Reale et al., 2007). Mixed-effects models are the current gold standard for partitioning variation into between- and within-individual variance components (Dingemanse and Dochtermann, 2013). Repeatability can be calculated for Gaussian data using linear mixed-effects models and non-Gaussian data using generalised linear mixed-effects models (GLMMs), although the latter case is less straightforward (Nakagawa and Schielzeth, 2010).

In movement ecology, repeatability has been used to compare the variation of exploratory behaviour in novel environments within and among individuals in the great tit (*Parus major*, Dingemanse et al., 2002), in the distance travelled per time unit (*Salvelinus confluentus*, Taylor and Cooke, 2014) or the variation in dispersal behaviour (Linyphiid spider (*E. atra*), Bonte et al., 2009). Reported values of repeatability for spatial behaviour ranged between $0.2 < R < 0.8$ for the distance traveled per time unit, whereas for dispersal behaviour repeatability generally reach values of $R < 0.2$ (Bell et al., 2009). In habitat selection behaviour, individual variability with respect to factors such as sex, age, reproductive status are well identified and easily accounted for by fixed variables (Manly et al., 2002). Variation among individuals in habitat selection behaviour has been reported for different species such as polar bears (*Ursus maritimus*, Arthur et al., 1996), wolves (*Canis lupus*, Hebblewhite and Merrill, 2008), grey seals (*Halichoerus grypus*, Aarts et al., 2008) or roe deer (Bonnot et al., 2015).

The particular structure of the data used in habitat selection studies in combination with the specific modelling approach might have hampered the ability of ecologists to quantify repeatability of the habitat selection behaviour. Movement trajectories are very suited in the context of repeatability because they can be seen as replications, in space and time, of habitat choices made by an individual. The statistical analysis of such a data requires a conditional logistic regression (CLR, Duchesne et al., 2010).

We identified two difficulties to overcome to partition variance into its between- and within-individual components for step selection functions (SSF, Thurfjell et al., 2014), a structurally related approach to RSF that links movement trajectories to environmental conditions. The difficulties are: (*i*) Estimates for the variances within and between individuals are not provided in easy-to-use software (Nakagawa and Schielzeth, 2010); and (*ii*) Browne et al. (2005) showed that the value of repeatability in such a framework is a function of the predictor variables, which means that the value of repeatability depends on the landscape characteristics of the selected sites and the available sites. This landscape dependence complicates comparisons of repeatability across sites that

differ in landscape structure.

Here, we develop a method to quantify repeatability in habitat selection based on SSFs with random effects accounting for variation in the response to environmental conditions between individuals and within an individual. Software typically used for step selection functions, such as the R packages *TwoStepClogit* (Craiu et al., 2012) or *coxme* (Therneau, 2012), allows only to specify between individual random effects. However, the implementation in standard software for Bayesian statistics such as jags (Plummer, 2003) or stan (Carpenter et al., 2016) is straightforward.

We derive the equation for repeatability from a threshold model formulation of the CLR model to illustrate the link between the CLR model and the components in the formula of repeatability. The threshold model formulation is used in discrete choice models widely used in economics (McFadden and Train, 2000). The random utility maximization framework underpinning these models provides a direct conceptual link between observed movement decisions and their underlying utility as perceived by the animal.

We evaluate the method for repeatability in habitat selection using SSF with simulated data. We then apply it to red deer in the Bavarian Forest National Park, Germany, showing that repeatability in habitat selection varies across sexes and time of day.

Materials and methods

Step selection functions

In step selection function analysis, the movement trajectory is represented as a series of discrete and conditionally independent movement decisions. At each (time-)step j an individual i can choose from a set of discrete proposal locations $S_{ij} = \{1, \ldots, K\}$. While this double discretisation (in time and in space) is somewhat artificial, it allows applying standard statistical techniques, in particular CLR. Each location k is assigned an SSF score $W(k)$ depending on the environmental features $x(k)$ of that location: $W(k) = \exp(\beta x(k))$, where β, the slope of the response to that environmental feature, is estimated from the data. The larger the SSF score, the higher the odds of the animal moving to that location. The probability of choosing a location k, is then given by (Fortin et al., 2005; Thurfjell et al., 2014):

$$\Pr(\text{location } k \text{ is chosen}) = \Pr(Y = k) = \frac{W(k)}{\sum_{l \in S} W(l)} \tag{III.2}$$

In addition to fixed factor effects, the necessity to account for among-individual variation in the study of habitat selection have been repeatedly emphasized (Gillies et al., 2006; Koper and Manseau, 2009; Duchesne et al., 2010). This can be done by integrating a random effect $v_i \sim \mathcal{N}(0, \sigma_v^2)$ that captures the variation between individuals. As the calculation of repeatability requires to estimate the variation within individuals we added a random factor $w_{ij} \sim \mathcal{N}(0, \sigma_w^2)$ that varies for the individual in each step. σ_v^2 is the variance among individuals and σ_w^2 is the variance within individuals. The score function is then:

$$W(k) = \exp((\beta + v_i + w_{ij})x(k)) \tag{III.3}$$

While, to our knowledge, standard software for random effects CLR cannot estimate the w_{ij}, the model can be readily formulated and implemented in standard software for Bayesian statistics (see Appendix). While it is tempting to directly use the estimations of the variances for σ_v^2 and σ_w^2 from equation III.3, this would overestimate repeatability because the residual variation from the discrete choice is not taken into account (Nakagawa and Schielzeth, 2010). In order to calculate variance partitioning, it is convenient to state the problem as a latent variable problem as is the custom in discrete choice modeling (McFadden, 1974). With this formulation we link the variances estimated by a CLR model to the components of the formula for repeatability.

Latent variable formulation of conditional logit models

It is assumed that the animals are rational and choose at each timestep the location with the highest benefit, which is called utility. Each location k is assigned a value for utility U_k. For the observer, the utility of the locations are not fully known, but they can be modelled as random variables with a fixed component that reflects the environmental features of a given location:

$$U_k = \beta x(k) + \epsilon_k \tag{III.4}$$

The familiar SSF score $W_k = \beta x(k)$ thus corresponds to the fixed component of the utility. The probability of choosing location k equals the probability that location k has the maximum utility of all available K alternatives. If the residuals ϵ_k are independent and identically distributed with a standard Gumbel distribution (i.e. extreme value type 1), then it can be shown (Maddala 1983, appendix 2) that the probability of choosing k is:

$$\Pr(Y = k) = \Pr(\max(U_1, \ldots, U_K) = U_k) = \frac{\exp(\beta x(k))}{\sum \exp(\beta x(l))} \tag{III.5}$$

i.e. we recover the same functional relationship as in the familiar SSF formulation.

In the formulation for the per individual per step, the utility U_{ijk} of location k for individual i at step j becomes:

$$U_{ijk} = (\beta + v_i + w_{ij})x(k_{ij}) + \epsilon_{ijk} \tag{III.6}$$

Ecologically, the parameter β stands for the average population-level utility with respect to covariate $x(k_{ij})$. v_i models the deviation of utility from the population mean for individual i, meaning that for some individuals the average utility may be higher or lower than β, the mean value of the population. The parameter w_{ij} adds variation to the individual mean in each time step, which allows some known degree of variability in the utilities. This data-level random slope effect w_{ij} (normally distributed with mean 0 and variance σ_w^2) accounts for heterogeneity in variance on the step-wise level. Such a step-wise heterogeneity is usually not assumed and the variance is supposed to be constant and to depend on the underlying distribution (e.g. in a Poisson-distributed random variable the variance equals the mean). However, if the assumption is not true, like in case of overdispersion where the variance in the data is larger than expected, a normally distributed random term in each step can account for this problem (Jiang, 2007).

For the purpose of simplification we will consider the choice between two sites, k and l. The probability that location k is chosen is equal to the probability that its utility is higher than that of location l:

$$\Pr(\text{location } k \text{ is chosen}) = \Pr(Y_{ijk} = 1) = \Pr(U_{ijk} > U_{ijl}) \tag{III.7}$$

By substituting equation III.6 in equation III.7 we obtain:

$$\begin{aligned}
\Pr(Y_{ijk} = 1) &= \Pr(U_{ijk} - U_{ijl} > 0) && \text{(III.8)}\\
&= \Pr((\beta + v_i + w_{ij})x(k_{ij}) + \epsilon_{ijk} - (\beta + v_i + w_{ij})x(l_{ij}) - \epsilon_{ijl} > 0) && \text{(III.9)}\\
&= \Pr((\beta + v_i + w_{ij})(x(k_{ij}) - x(l_{ij})) + \epsilon_{ijk} - \epsilon_{ijl} > 0) && \text{(III.10)}
\end{aligned}$$

Hence, the probability of choosing location k is determined by the environmental features at the two locations, as all parameters (β, v_i, w_{ij}) are the same for individual i for all locations at timestep j.

The CLR model III.2 can now be formulated as a threshold model (Snijders and Bosker,

2012):

$$Y_{ijk} = \begin{cases} 1, & \text{if } y'_{ij}(k,l) > 0 \\ 0, & \text{if } y'_{ij}(k,l) \leq 0 \end{cases} \tag{III.11}$$

where the unobserved latent random variable $y'_{ij}(k,l)$ is a function of the difference of the covariates $\Delta x_{ij}(k,l) = x(k_{ij}) - x(l_{ij})$ at two locations, namely:

$$\begin{aligned} y'_{ij}(k,l) &= (\beta + v_i + w_{ij})(x(k_{ij}) - x(l_{ij})) + \epsilon_{ijk} - \epsilon_{ijl} && \text{(III.12)} \\ &= \Delta x_{ij}(k,l)\beta + \Delta x_{ij}(k,l)v_i + \Delta x_{ij}(k,l)w_{ij} + r_{ij}(k,l) && \text{(III.13)} \end{aligned}$$

where the residuals $r_{ij}(k,l)$, the difference of two standard Gumbel-distributed random variables, follows a standard logistic distribution. The outcome of the observable dichotomous random variable Y_{ijk} is thus determined by the value of the underlying latent continuous random variable y'_{ij}, which is a function of covariates $x(k_{ij})$, where parameters β, v_i, w_{ij} are fixed within a stratum.

Repeatability for mixed conditional logit models

Repeatability is the fraction of total variation due to variance between individuals. To calculate this value we need to decompose the sources of variation in the selection making process. The variation in the selection making process is the variance of the unobserved latent variable $y'_{ij}(k,l)$ (Snijders and Bosker, 2012). The variance of $y'_{ij}(k,l)$ can be decomposed to

$$\text{var}(y'_{ij}(k,l)) = (\Delta x_{ij}(k,l))^2\sigma_v^2 + (\Delta x_{ij}(k,l))^2\sigma_w^2 + \text{var}(r_{ij}(k,l)) \tag{III.14}$$

given that $\Delta x_{ij}(k,l)$, v_i and w_j are independent of each other. σ_v^2 is the variance among individuals and σ_w^2 is the variance within individuals. $\Delta x_{ij}(k,l)$ is the difference of the covariate between positions k and l. The variance of the residuals $\text{var}(r_{ij}(k,l))$ follows a logistic distribution and equals $\pi^2/3$.

Finally, for two locations k, l with $l \neq k$ a formula for repeatability can be derived:

$$R(k,l) = \frac{(\Delta x_{ij}(k,l))^2\sigma_v^2}{(\Delta x_{ij}(k,l))^2\sigma_v^2 + (\Delta x_{ij}(k,l))^2\sigma_w^2 + \pi^2/3} \tag{III.15}$$

Hence, the value of repeatability depends on the strength of the environmental gradient between the two locations k and l (Browne et al., 2005). This makes ecological sense in that differences in behavioural variations will be more pronounced as the environmental

gradient becomes steeper. Two extremes can be distinguished: As the environmental gradient vanishes, i.e. the two sites are equivalent from the point of view of the observer, repeatability approaches zero. In contrast, in the limit of an infinitely large environmental gradient between the two locations, the habitat choice of the individual becomes *de facto* deterministic also from the point of view of the observer, and repeatability simplifies to the familiar $R(k,l) = \sigma_v^2/(\sigma_v^2 + \sigma_w^2)$.

Evaluation with simulated data

We tested the method on simulated data with known parameter values. A one-dimensional covariate of the location data was sampled from a landscape with uniformly distributed resources ($x(k) \sim unif(0,1)$). Movement trajectories were simulated with a fixed value for the selection coefficient $\beta = 1$ but different values for the variation between individuals σ_v (0.1, 0.2, 0.5, 1, 2, 3) and within individuals σ_w (0.1, 0.2, 0.5, 1, 2, 3), numbers of steps per individual (10, 25, 50, 100) and numbers of individuals (5, 10, 15, 20).

We estimated model parameter by fitting the model

$$\Pr(Y_{ij} = k|\beta, \sigma_v, \sigma_w) = \frac{exp((\beta + v_i + w_{ij})x(k_{ij}))}{\sum_{l \in S_{ij}} exp((\beta + v_i + w_{ij})x(l_{ij}))} \tag{III.16}$$

using *jags* (Plummer, 2003) in R (R Core Team, 2015) and the R package *R2jags* (Su and Yajima, 2014). As prior for the selection coefficient β we used a normal distribution with mean 0 and standard deviation of 100. For the hyperpriors of the random effects we chose a gamma distribution with shape parameter 1 and scale parameter 1/3. The R Code is available in the attachment. Convergence of chains was tested with Gelman-Rubin convergence diagnostics. We considered MCMC chains as converged when the potential scale reduction factor the Gelman-Rubin diagnosis was less than 1.05.

Illustration with observed data

Landscape description

The study area is located in the Bavarian Forest national park, which lies in south-eastern Germany along the border between Czech Republic and Germany (center coordinates: $49\,°3'19''N, 13\,°12'9''E$). We estimated vegetation cover from airborne LiDAR data acquired using a Riegl LMS-Q 560 system operating with a wavelength of 1,550 nm. Leaf-off data were acquired between April 2008 and November 2009 from the entire national park area with an average point density of 9.8 points/m^2. LiDAR measurement points were grouped into 5×5 m grid cells. For each grid cell, we calculated inverse penetration ratios

Tab. III.1 Overview of red deer data used in the analysis. For month June we analysed the data of 11 females and 8 males. For each individual we used 50 locations.

Sex	Day		Twilight		Night	
	#Indiv	#Positions	#Indiv	#Positions	#Indiv	#Positions
Females	11	550	11	550	11	550
Males	8	400	8	400	8	400

at a height of 2-60 m above ground. This inverse penetration ratio is an estimation of the fractional vegetation cover at this height (see Ewald et al., 2014, for more information), and hence a suitable measure of habitat cover for ungulates (Lone et al., 2014).

Location data of red deer

Location data were derived from 11 female and 8 male red deer fitted with GPS (Global Positioning System) collars in two subsequent years (2006/2007). We captured animals while staying in winter enclosures by luring them in box traps with side windows. The procedure was approved by the Government of Upper Bavaria, Germany.

In the analysis we used only data from June, to reduce possible seasonal variations. Time difference between steps was at least 2 hours. GPS-data was further partitioned according to time of recording in A) daytime (8-15h), B) night (22-2h) and C) twilight(16-21h, 3-7h). We sampled 10 random locations for each recorded location based on empirical distribution of turning angle and step lengths given by all other animals but the focal individual. The distributions were calculated separately for time period of day: daytime, night, twilight, as time of day is known to influence movement behaviour of animals (Owen-Smith et al., 2010). For random point sampling we applied the package *hab* (Basille, 2014). The data set consisted of exactly 50 locations per individual and time period of the day for the analysis (N=2,850, see Tab. III.1 for details). We calculated repeatability of habitat selection behaviour for daytime, night and twilight, and separately for each sex.

Results

Simulation

For the simulated data, convergence differed across different parameters: chains for β and σ_v converged after 20,000 iterations, but for σ_w, i.e. the variation within individu-

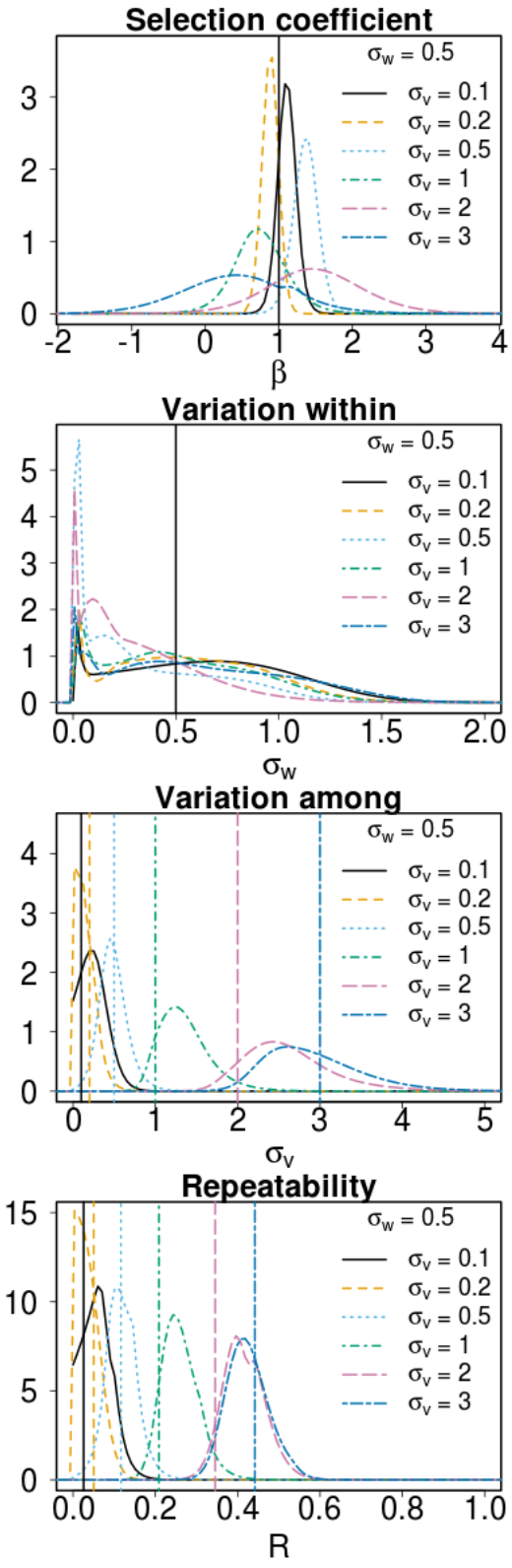

Fig. III.1 Posterior distributions for variation within σ_w and among σ_v, β and the resulting value of repeatability R on the link scale for simulated paths of 15 individuals with for each 100 steps given values for σ_v (0.1, 0.2, 0.5 , 1, 2, 3), as well as a fixed value for the general selection $\beta = 1$ and variation within individuals $\sigma_w = 0.5$.

als, the number of iterations required for convergence increased with the number of steps of an animal: for 10 steps 20,000 iterations were sufficient, for 100 steps per individual 220,000 iterations were needed. The number of individuals also affected the convergence behaviour slightly negatively. In contrast, the value of the parameters σ_v and σ_w apparently did not influence the convergence behaviour of the chains (Appendix S2). As expected, the precision of the estimates increased with the number of individuals and the number of steps per individual. Also the value of the parameters σ_v and σ_w influenced the precision of the estimates (see below for details).

True values were in almost all cases within the 95% posterior credible intervals of the estimates (Fig. III.1, Appendix S2). As the expected values of σ_v and σ_w increased (e.g. $\sigma_v = 3$) posterior distributions for all estimated parameters became flatter. However, for repeatability the effect was less pronounced since repeatability is not a linear function of σ_v and σ_w. In particular, large values of either σ_v or σ_w with large 95% posterior credible intervals did not translate into a as large as 95% posterior credible interval for repeatability.

Repeatability for red deer

According to the Gelman-Rubin diagnostics all chains converged after 250,000 iterations. The high number was needed as the chains of σ_w were highly autocorrelated.

The posterior distributions of the selection coefficient differed substantially between day and night for male and female red deer as the corresponding posterior distributions hardly overlap (Fig. III.2). During the night, sites with low cover were strongly selected (median $[2.5\%, 97.5\%]$-quantiles of β for females: -3.11 $[-4.04, -2.44]$, for males -1.94 $[-2.98, -0.93]$), whereas during the day selected sites were characterized by higher cover (mean of β for females: -0.13 $[-1.45, 1.16]$, for males 0.33 $[-0.48, 1.06]$). For twilight the estimated selection coefficient was between the value for day and night (mean of β for females: -1.34 $[-2.16, -0.59]$, for males -0.72 $[-2.01, 0.55]$). In general estimated selection coefficients were lower for females, meaning that females selected open areas more strongly than males did, which was even more pronounced during the night.

For males, the posterior distributions of the variation of habita selection for cover within individuals σ_w was similar for night (0.62 $[0.04, 2.07]$), day (0.88 $[0.05, 2.08]$) and twilight (0.75 $[0.04, 1.85]$). For females, distributions for σ_w were similar for night (0.8 $[0.05, 2.12]$) and day (0.62 $[0.03, 1.92]$). Although the variance within individuals was higher for twilight (1.51 $[0.06, 2.75]$), then during night and day, the difference was not significant. In general, posterior distributions of the variation within individuals were

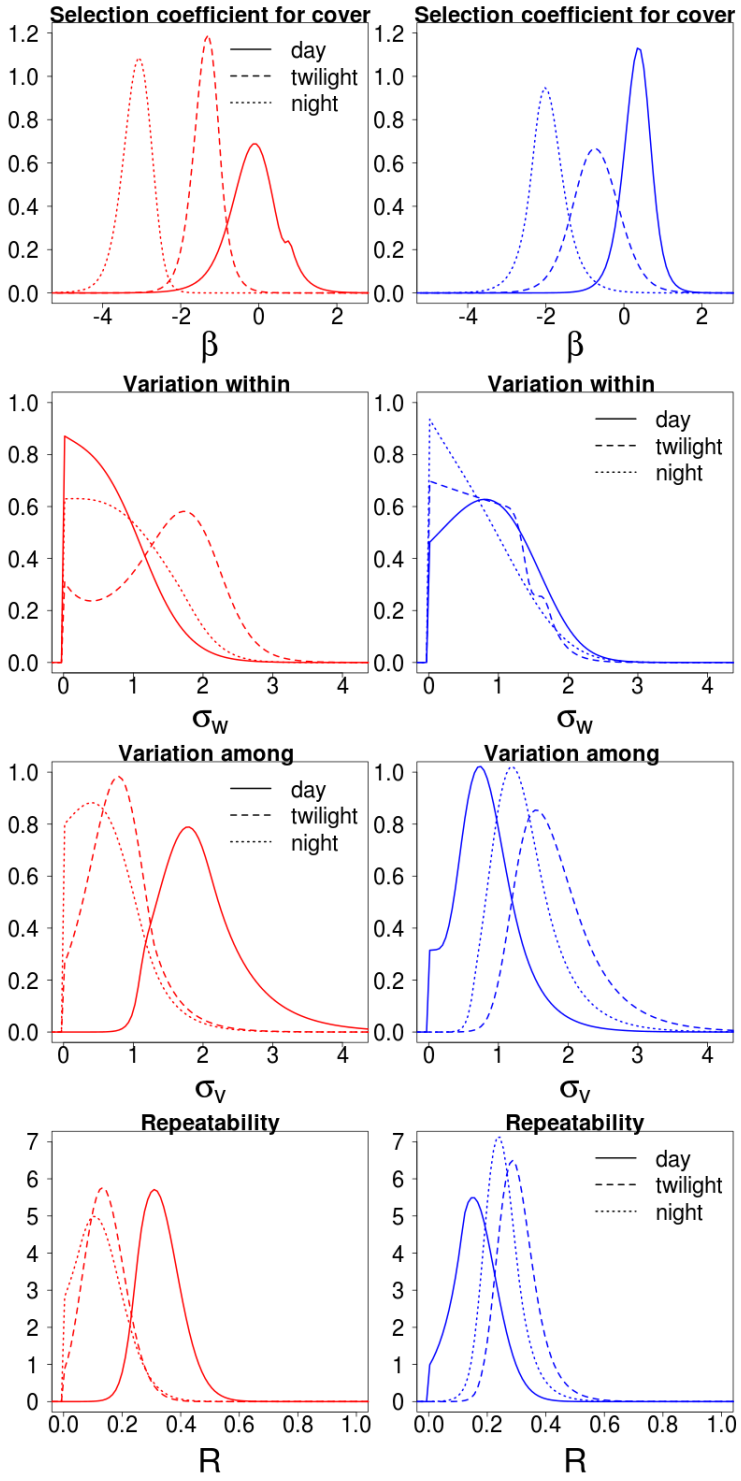

Fig. III.2 Selection of sites characterized by cover of red deer individuals (10 males, 10 females) over different timeperiods of the day (day, night, twilight) in June. For each timeperiod 50 relocations for each individual were used. Posterior distributions were ascertained after 250,000 iterations of the mcmc-run based on a Bayesian framework. Posterior distributions of the selection coefficient β (first column), variation within σ_w (second column) and among individuals σ_v (third column) and repeatability on the link scale (last column). First row shows results for females, second row for males.

skewed toward low values, except for males at day, which was unimodal (peak at ≈ 1) and that for females at night, which was bimodal (one peak at 0 and one peak at ≈ 1.7).

Posterior distributions for the variation among individuals σ_v were all unimodal, but had different median values. For females highest values σ_v were found at day (1.9 $[1.11, 3.56]$), while distributions for twilight (0.77 $[0.1, 1.86]$) and night (0.58 $[0.04, 1.77]$) were rather similar. For males, highest value decreased from twilight (1.73 $[1, 3.29]$), to night (1.31 $[0.69, 2.66]$) and day (0.79 $[0.09, 1.9]$). The most obvious discrepancy was found for the variation among individuals σ_v during the day. Female red deer differed the most among each other in their habitat selection behaviour during the day, when males selected similar sites with respect to cover. Differences in site selection with respect to cover for male red deer were the highest during twilight.

Overall, the distributions of repeatability (Fig. III.2), derived from variation within and among individuals, was unimodal for all time-periods and both sexes. Values for repeatability were highest for females during the day ($0.32[0.21, 0.49]$), when males exhibited the lowest values ($0.16[0.02, 0.32]$). Repeatability in habitat selection behaviour of males at night ($0.25[0.15, 0.4]$) and twilight ($0.3[0.19, 0.46]$) did not differ statistically, while for females distributions of repeatability values for twilight ($0.14[0.02, 0.29]$) and night ($0.12[0.01, 0.3]$) were very similar.

Discussion

Estimating Repeatability: model performance

Mixed effects models have become the approach of choice for repeatability quantification, and extensions from linear to generalized linear models exist (Nakagawa and Schielzeth, 2010). Here, we extend the class of covered models to mixed CLR, which is commonly used in SSF analyses (Thurfjell et al., 2014). This extension allows the quantification of repeatability in habitat selection behaviour of animals by using movement trajectories.

We have shown that repeatability of habitat selection explicitly depends on environmental conditions. The reason is that within- and between individual variability is estimated with respect to their response to environmental conditions. Due to the particular structure of CLR models, random effects apply to the regression coefficients (slope) because there is no intercept (Duchesne et al., 2010). Values of repeatability therefore need to be accompanied by information describing the environmental conditions they were calculated, such as minimum and maximum value of the factor. We suggest to use the longest reasonable environmental range in order to not artificially reduce repeatability.

Recently, Leclerc et al. (2016) estimated for the first time repeatability in habitat selection of brown bears (*Ursus arctos*) using resource selection functions (RSF). They overcame the problem of estimating the within-individual variation in the selection of a habitat by referring it to the variation in the selection between years for an individual. However, in the case of no variation between the years, this approach would not detect any within-individual variation even if there was a high within-individual variation in habitat selection.

The within-individual variation in habitat selection, σ_w, is directly estimated in our approach as part of the model fitting. The inconvenience of our approach is that the model currently needs to be implemented as a Bayesian model in software such as jags (Plummer, 2003) or stan (Carpenter et al., 2016). However, an advantage is that it provides an uncertainty estimate of repeatability (Nakagawa and Schielzeth, 2010). An alternative and arguably simpler way to calculate point estimates of within-individual variability is to first fit a statistical model, and then calculating the standard deviation of model residuals for each individual (e.g. Briffa et al., 2013). However, the simpler alternative approach risks inflating type I error by ignoring any uncertainty in the estimate and makes the implicit assumption of homoscedasticity (residuals have the same variance for all individuals, Cleasby et al., 2014). In addition, unbalanced sampling of individuals may affect the outcome as individuals with more data will contribute more strongly to the outcome (Gillies et al., 2006). Mixed effect models provide a solution to this as such models decompose the variance into among and within individual variation by simultaneously accounting for unbalanced sampling schemes (Dingemanse and Dochtermann, 2013). As SSF can be regarded as a special case of RSF (Potts et al., 2014) the proposed framework can easily be generalised to RSF.

Repeatability rests upon the estimates of variation within and between individuals, σ_v and σ_w. The values of these variances may be strongly influenced by the choice of model structure and by the sampling regime. The aim of repeatability is to identify consistent differences between individuals rather differences in conditions that individuals are exposed to which leads to pseudo-repeatability. Pseudo-repeatability is a bias in the repeatability estimate due to differences in the measurement conditions (Westneat et al., 2011). This is especially a problem when dealing with behaviour that is measured in the field where various variables may influence the behaviour under study. Here, we paid particular attention not to vary too many factors in the field data. For example, we ensured that for every time slot we analysed the very same individuals and the exactly same number of time steps (50). In general, Dingemanse and Dochtermann (2013) showed that pseudo-repeatability can be avoided by either including a between-individual fixed

covariate capturing variation due to biased sampling, or by including additional random effects which can be accomplished within the proposed framework.

Repeatability of red deer habitat selection behaviour

We applied our model to male and female red deer monitored in the Bavarian National Park, Germany, to estimate within- and between-individual variability of habitat selection behaviour, as well as its repeatability (R). Both sexes selected for open areas at night and twilight although females did so to a greater extent than males (Fig. 2). In June, most females are breeding a calf and face high energy requirement, and seek at night habitats providing them with abundant and high quality forage they find on open areas (Bonenfant et al., 2004) to cope with this high energy demand. This between-sex difference in habitat selection behaviour was also apparent in the estimated variation among individuals, whereby males showed moderate values for σ_v with little variation over the course of the day. On the contrary, if females had the largest among-individual variability during the day, σ_v was the smallest at night and twilight (Fig. 2), meaning that almost all females are consistent in selecting for open habitats outside of daytime. This result suggests a strong constrain on habitat selection of female red deer, again, likely associated with the costs of breeding and milking calves at this crucial time of the year (Clutton-Brock et al., 1984). The resulting R values of repeatability mostly mirrored the among-individual patterns in the two sexes, being less variable for males among the three time periods we considered (Fig. 2). Ranging between 0.12 and 0.32, and 0.16 and 0.30 for males and females respectively, repeatability of habitat selection for red deer seems to be slightly smaller than 0.37 the average value of repeatability calculated in a review over all behaviours (Bell et al., 2009). This consistent among-individual differences in habitat selection for cover we report suggest a potential for selection on this behavioural traits (Reale et al., 2010), which is supported by the evolutionary changes observed in the ranging behaviour of elk (*Cervus elaphus*) in response to hunting (Ciuti et al., 2012). In our study, a combination of human-disturbance during the day along with the low mobility of calves could force female red deer to a restricted ranging behaviour and hence, to a very low variation of habitat selection for cover during the day for a given female (low σ_w). Among-individual variation hence reflects the variability in home range composition which, in turn, could make the highest R value found for habitat selection of females during the day an environmental constraint rather than an evolutionary potential for selection. Repeatability values should be interpreted carefully, in association with within- and among-individual variation.

Conclusion

GLMMs have been used and proven to decompose the observed variance in a behaviour into between- and within-individual variation (Dingemanse and Dochtermann, 2013). We have extend its application for the behaviour of habitat selection in the framework of SSF, which can be generalised to RSF. A quantification of the between- and within-individual variation in habitat selection behaviour is necessary to asses the plasticity of a species towards changing conditions in the face of global change, showing the importance of an improved understanding about animal movement for wildlife management. Within-individual variance refers to the consistency in the behaviour of individuals, which is the prerequisite for the heritability of a trait. Differences in behaviour between individuals must be consistent so that selective pressure can act. Hence, only if the degree of consistency in individual variation is evaluated, the ecological and evolutionary implications of habitat selection behaviour can be assesed (Sih et al., 2012).

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Supplementary material to "Quantification of repeatability in habitat selection behaviour" by Claudia Dupke et al.

Appendix S1 R-Code. R-Code and JAGS-Code for calculating values for repeatability on simulated data.

```
#' Calculating the fraction of variation due to between-individual and
#'  within-individual variability
#'
    ================================================================================

sink("ssfmodel_both.txt")
cat("
model{
    # priors
    sigma_a ~ dunif(0, 1000)
    sigma_w ~ dunif(0, 1000)
    tau_a <- 1 / (sigma_a * sigma_a)
    tau_w <- 1 / (sigma_w * sigma_w)
    beta ~ dnorm( 0, 0.01)

    #Likelihood
    for (i in 1:m) { # m: number of individuals
                u_a[i] ~ dnorm(0, tau_a) # Among-individual random
                    effect
    }
    for (i in 1:n) { # n: number of steps
        u_w[i] ~ dnorm(0, tau_w) # Within-individual random effect,
            overdispersion
        for (j in 1:alternatives) {
                        w[i, j] <- exp((beta + u_w[i] + u_a[individual[
                            i]]) * X[(i-1)*alternatives + j])
        }
        p[i] <- w[i, selected[i]] / sum(w[i,])
                # Bernoulli error
                y[i] ~ dbern(p[i])
    }
    }
    ", fill = TRUE)
sink()


init_fn_both <- function() {
  list(
    "beta" = 0,
    "sigma_a" = 1,
    "sigma_w" = 1
  )
}

#' Simulates step selection
#' x: environment, e.g. forest cover, takes values between 0 and 1
sim_ssf <- function(b, sd_a = 0, sd_w = 0, m = 10, step_count = 50, K =
    20) {
  # b: slope of selection
  # sd_a: among-individual variation
  # sd_w: within-individual variation
  # m: number of individuals
```

```r
  # step_count: number of steps per individual
  # K: number of alternative steps per step
  x <- matrix(runif(K * step_count * m), ncol = K)
  #standardize
  #x <- (x-mean(x))/sd(x)
  b_as <- rnorm(m, mean = 0, sd = sd_a)
  b_a <- rep(b_as, each = step_count)
  b_w <- rnorm(step_count * m, mean = 0, sd = sd_w)
  w <- exp((b + b_a + b_w) * x)
  p <- w / rowSums(w)
  selected <- apply(p, 1, function(x) sample.int(K, size = 1, prob = x))
  list("x" = x, "b_a" = b_as, "b_w" = b_w, "selected" = selected,
       "b" = b, "sd_a" = sd_a, "sd_w" = sd_w, "m" = m, "step_count" =
          step_count, "K" = K)
}

#' Extract data in a format suitable for jags for simulated data
get_jags_data_sim <- function(ssf_data) {
  list("m" = ssf_data$m,
       "n" = nrow(ssf_data$x),
       "alternatives" = ssf_data$K,
       "X" = as.vector(t(ssf_data$x)),
       "selected" = ssf_data$selected,
       "y" = rep(1, nrow(ssf_data$x)),
       "individual" = rep(1:ssf_data$m, each = ssf_data$step_count))
}

library(R2jags)
K <- 10 # number of alternative steps
step_count <-  25# number of steps per animal
m <- 10 # number of animals
b <- 0.5 # slope
sa <- 0.3 # among individual variation (standard deviation)
sw <- 0.2 # within individual variation (standard deviation)

#' Simulations with between-individual and within-individual random
    effect
set.seed(2)
data <- sim_ssf(b, sd_a = sa, sd_w = sw, m = m, step_count = step_count,
     K = K)
jags_data <- get_jags_data_sim(data)
set.seed(2)
#' Parameter estimation
jags_both_full <- jags(data = jags_data, inits = init_fn_both,
                               parameters.to.save = c("beta", "sigma_a",
                                  "sigma_w","u_w", "u_a"),
                               model.file = "ssfmodel_both.txt", n.chains
                                    = 10, n.iter = 2000, n.burnin = 1000,
                                    n.thin = 10)
#' plot results
par(mfrow=c(1,3),cex.lab=1.5,cex.axis=1.5,las=1)
plot(density(jags_both_full$BUGSoutput$sims.list$sigma_w,na.rm=TRUE),
                main=paste("Posterior s within "),xlab="s within")
abline(v=sw,col="red")
plot(density(jags_both_full$BUGSoutput$sims.list$sigma_a,na.rm=TRUE),
                main=paste("Posterior s among ",sep=""),xlab="s among")
abline(v=sa,col="red")
plot(density(jags_both_full$BUGSoutput$sims.list$beta,na.rm=TRUE),
                main=paste("Posterior beta ",sep=""),xlab="beta")
abline(v=b,col="red")
```

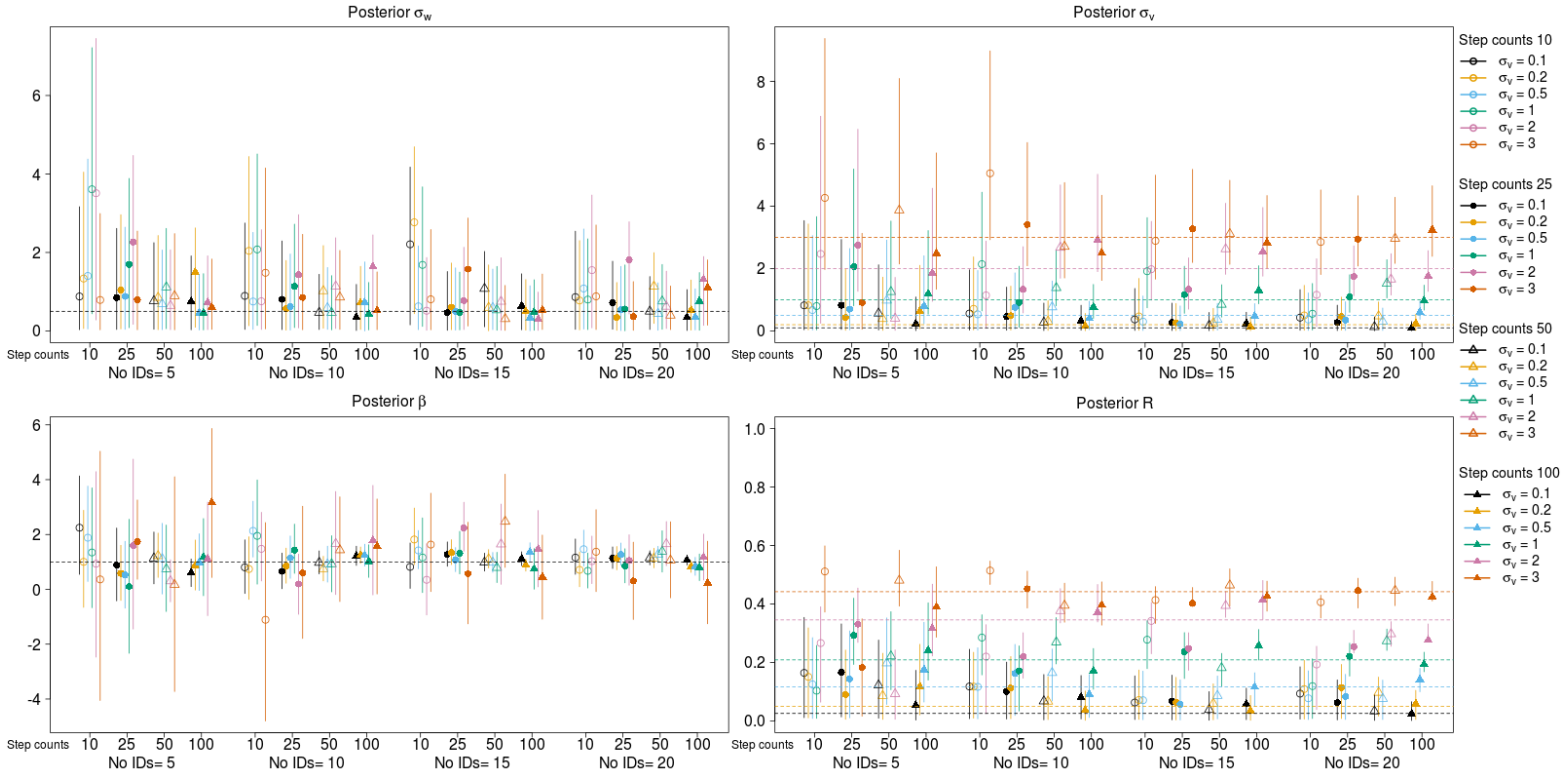


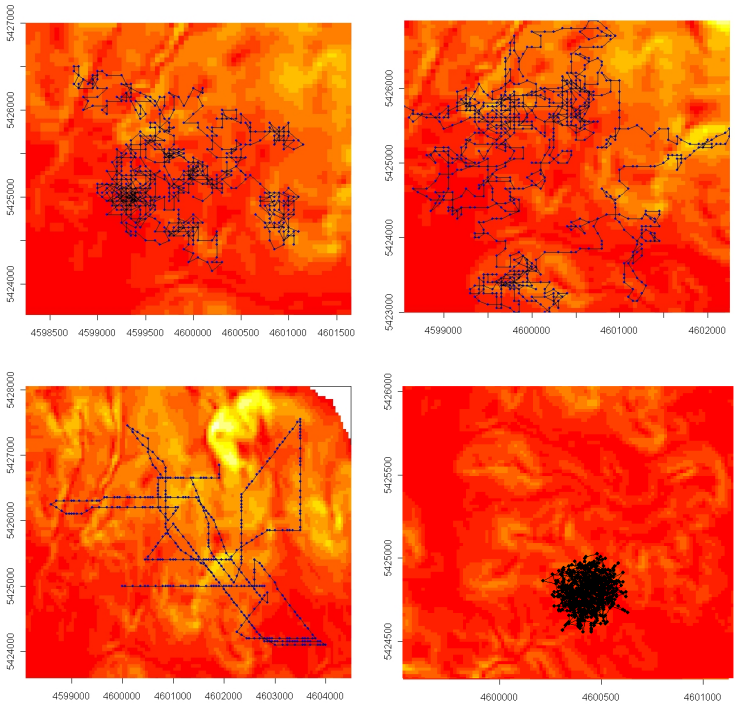
Figure 1: **Appendix S2 Test of performance.** Boxplots show median and 95 percent quantiles of the posterior distributions after 220,000 iterations of mcmc-sampling given simulated data. Data were simulated with fixed values for $\sigma_w = 0.05$ and $\beta = 1$ and different values for σ_v, which were 0.1, 0.2, 0.5, 1, 2, 3, number of individuals (No IDs), which were 5, 10, 15 or 20 and the number of steps (Step counts) per individual, which were 10, 25, 50 or 100. Lines assign the to be estimated true value. Colours link the true value with the estimated values from the Bayesian framework using mcmc-sampling of 220,000 iterations. Values of repeatability were calculated from the estimated values of σ_v and σ_w and are compared with the theoretically expected value that is shown as a line in the respective colour.

Research paper IV

Claudia Dupke, Florian Hartig, Marco Heurich, Björn Reineking

On the move: Modelling habitat selection of large herbivores

Summary: We propose a spatially-explicit discrete non-linear individual-based movement model that produces realistic patterns on the population level.



Authors affiliation:

Claudia Dupke*[1], Florian Hartig[2] Marco Heurich[3,4], Björn Reineking[1,5],

[1] Biogeographical Modelling, Bayreuth Center of Ecology and Environmental Research BayCEER, University of Bayreuth, Universitätsstr. 30, 95440 Bayreuth, Germany

[2] Department of Biometry and Environmental System Analysis, University of Freiburg, Tennenbacher Str. 4, 79106 Freiburg, Germany

[3] Chair of Wildlife Ecology and Management, University of Freiburg, Tennenbacher Str. 4, 79106 Freiburg, Germany

[4] Department of Research and Documentation, Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany

[5] Université Grenoble Alpes, Irstea, UR EMGR 2 rue de la Papeterie BP 76, 38402 St-Martin-d'Héres, France

* corresponding author

Summary

Patterns of animal movement data are analysed to understand animal behaviour. Movement patterns on the population level can be described with respect to environmental conditions, albeit we are not able to understand the ultimate motivation of animal movement. New conceptual frameworks in the field of movement ecology seem to be promising to support in understanding the behavioral process of movement. In particular, individual-based movement models (IBMM) that focus on the individual and models its internal state have been capable of linking patterns on the population level to behavioral processes on the individual level. In this study, we set up a discrete non-linear IBMM that combines the framework of the traditional method of resource selection functions and IBMM. GPS-based position data of roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) recorded from 2002 to 2012 in the Bavarian Forest National Park, Germany, were used to parameterize the model with generalized mixed effect models. Forward-simulation of the parameterized model were used to validate the model, by comparing observed with simulated patterns on the population, such as home range size and distribution of step length. We further followed a pattern-oriented approach by testing whether diurnal variation of attraction to and repulsion from environmental factors like buildings, roads, home range centre, food and cover availability are analogous for empirical and simulated data. The forward simulation provided realistic pathways with respect to the patterns under study. Our approach illustrates a feasible combination of forward- and reverse-modelling.

Introduction

GPS-based positions of animals provide an insight to impressive patterns of animal ecology such as home range formation (Moorcroft et al., 2006; Kie et al., 2010), resource use (Manly et al., 2002; Boyce et al., 2002), dispersal (Mueller and Fagan, 2008; Cagnacci et al., 2011) and population dynamics (Morales et al., 2010). These patterns are usually analysed on the population level by using descriptive and rather static approaches. For example, resource use of animals is most commonly investigated using resource selection functions (RSF) where characteristics of the population is averaged (Johnson et al., 2002). Nonetheless, RSF studies can give reliable answers to the question of "When and where do animals move" as with these spatio-temporal patterns of the underlying movement process can be detected. However, the question of "Why do they move" which occupies researchers for more than three decades (*e.g.* Johnson, 1980; Manly et al., 2002; Rota et al., 2013), remains a challenge. Traditional inferential methods seem to be not capable of entangling the links between behavioural processes, environmental conditions and patterns on the population level. This is where the emerging field of movement ecology may provide new approaches by leaving the population level and focussing on the individual that ultimately produces these patterns on the population level (Nathan and Giuggioli, 2013).

One approach is to integrate a description of the internal state of an animal in the analysis, which provides clues about the *why*. The internal state can be regarded as a multidimensional vector described by temporal varying characteristics such as gut fill, energy reserves, reproductive status, etc. (Nathan et al., 2008). The internal state is assumed to indicate the motivation and readiness to move. Clearly, variables of the internal state can hardly be measured in the field. Therefore, models have been developed that account for variation in the internal states. These models are called individual-based models (IBM, Grimm and Railsback, 2005).

Method

We have set up a discrete non-linear individual-based movement model (IBMM) that combines the framework of RSF and IBMM. The framework is flexible in terms of model rules where movement is modeled as a stochastic relocation process (Avgar et al., 2013). Given the current location and a set of potential targets, probability of selecting one of the potential targets is based on the so-called redistribution-/ displacement-/ movement-kernel (Avgar et al., 2013; Dalziel et al., 2008). This probability-kernel is proportional to

a link-function of the drivers of animal movement in focus. For parameter estimation we applied computationally efficient generalized additive mixed effects models following the concept of RSF (Craiu et al., 2011). Parameter may vary according to the elevation of the sun or the time of the day, respectively, using a time-varying coefficient model instead of state-switching for changing animal behaviour over time (Hastie and Tibshirani, 1993).

Covariates

In our model movement decisions are based on the probability of the presence of the animal. We therefore chose covariates that influence the site selection of an individual based on literature: distance to roads (Bjørneraas et al., 2012; Coulon et al., 2008), distance to buildings (Coulon et al., 2008) and attractivity of forage and cover availability (Benhaiem et al., 2008; Mysterud et al., 1999; Pellerin et al., 2010; Linnell et al., 2004; Bongi et al., 2008; Panzacchi et al., 2010; Houston et al., 1993; Godvik et al., 2009; Creel and Winnie, 2005). Roe deer and red deer exhibit stable home ranges throughout the summer (Linnel and Andersen, 1995). We accounted for this by including the distance to the home range centre which is calculated as the mean of the x- and y-coordinates of the relocation data.

Model

The discrete nonlinear varying coefficient model provides rules that steer individuals through a spatially explicit landscape.

State variables and scales

The landscape is represented by a grid with a grid cell size of $50 \times 50m^2$. Individuals are characterized by ID, sex, its home range centre and a perceptual range. As we work with territorial animals the individuals are assumed to know the whole area.

Process overview and scheduling

In brief, one model step consists of the following substeps:

1. Set the time $T_{t+1} = T_t + \Delta t$.
2. Update parameter.

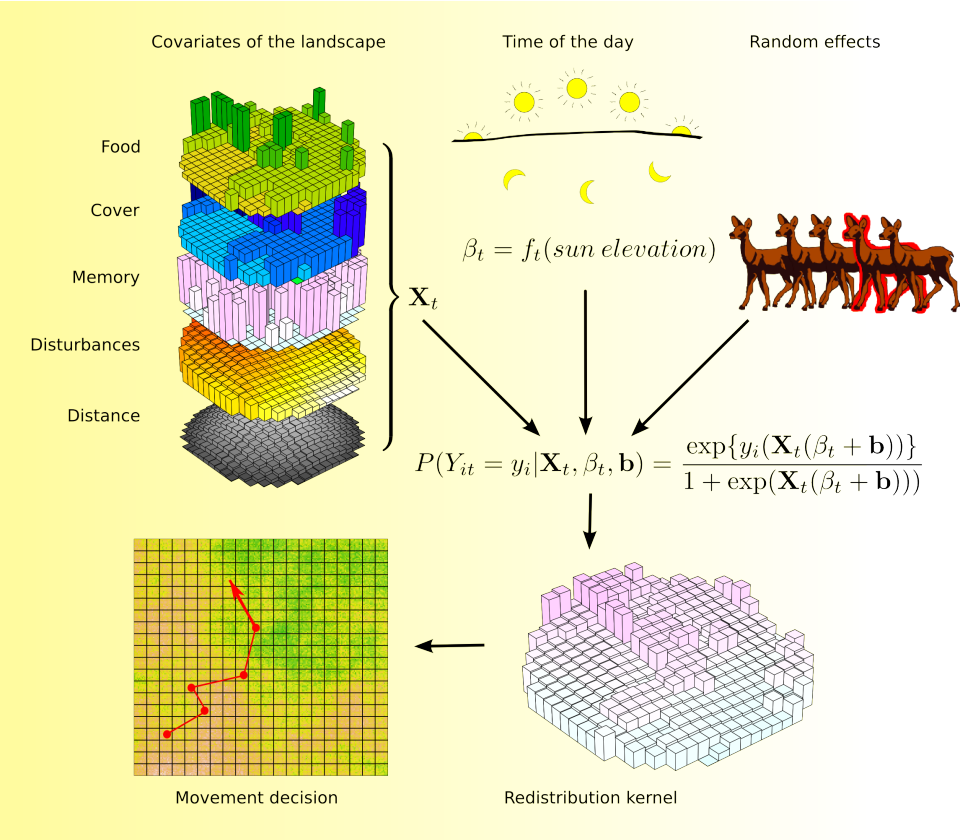


Figure IV.1: Model overview shows the components and the process of the simulation. Given a current position, some covariates that describe the conditions of the surrounding, the time of day, a specific individual and some earlier estimated parameters, probabilities for each cell in the surrounding are calculated (redistribution kernel). Based on the probabilities, one cell is selected randomly. Iterations of this process create a simulated path.

3. Get landscape and location-based information about each grid cell in the perceptual range of the animal.

4. Calculate a selection probability for each cell within the perceptual range.

5. Select one cell by random given the former calculated probabilities.

6. Go to 1.

In greater detail:

1. In our analysis we chose a time lag of one hour between two successive steps.

2. One fundamental element of our model is time. In particular, for each time step we calculated the sun elevation. Sun elevation was standardized with respect to the maximum and minimum sun elevation in spring/summer (April - August). By excluding a possible seasonal effect we ensure focussing on the diurnal effect. Usually, time-varying behaviour of movement is accounted for by incorporating different states in the field of state-space-modelling, which requires a Bayesian framework and computationally expensive MCMC methods to estimate parameters. We circumvented this problem by using time-varying parameters. As we wanted to describe time-varying behaviour over the day we used cyclic B-splines to describe variation over time/sun elevation. Fourier basis functions could equally be used. With such an varying-coefficient model (Hastie and Tibshirani, 1993) we can employ the computationally efficient generalized mixed effect model (GLMM) approach to analyse parameters. For each covariate which are explained in 3) we incorporate a set of parameters that determines the variation of relevance for the movement decision.

3. Landscape characteristics at a potential target are presumably strong drivers of movement decisions. The landscape is characterized by the availability of biomass, the degree of cover and the proximity to buildings and roads. Location-based information are statistics that relate the current position to potential target cells namely distance, turning angle and the distance to the fixed home-range centre. The set of potential target cells equals all cells within a fixed radius around the current position of the animal.

4. Given the covariates and the corresponding parameters, probability of individual n selecting cell Y_i at time t is calculated using the logit link

$$P(Y_{nit} = y_i|\mathbf{X}_{nt}, \boldsymbol{\beta}_{nt}) = \frac{\exp(\mathbf{X}_{nt}\boldsymbol{\beta}_{nt})}{1 + \exp(\mathbf{X}_{nt}\boldsymbol{\beta}_{nt}))} \tag{IV.1}$$

where y_i is a vector of binary responses, $y_i = 1$ if i is visited, $y_i = 0$ otherwise. Landscape, location-based and memory information for cell j are stored in the jth row of covariate matrix X with k columns. $\boldsymbol{\beta}_t = (\beta_{1t}, \beta_{2t}, \ldots, \beta_{kt})'$ is a vector containing the time-varying coefficients, whith $\boldsymbol{\beta}_{nt} = \mathbf{f}_n(t)$ and $\beta_{nwt} = f_{nw}(t) = \sum_{p=1}^{z} B_p^m(t)(\gamma_{wp} + b_{nwp})$, where z is the number of basis functions building the spline and $B_p^m(t)$ are recursively defined basis functions, see (Wood, 2006, p.152) for more details. The coefficients $(\gamma_{wp} + b_{nwp})$ represent the mixed effects structure of the model: γ_{wp} is the population mean (fixed effect) and b_{nwp} is the animal-level random effect. The random effects are independent and multivariate normally distributed with mean $\mathbf{0}$ and a diagonal variance matrix, assuming no covariance to occur.

5. Given the probabilities for each potential target cell i from equation (IV.1) one cell is chosen to be the realized position in the next time step.

Model parameterization

For each of the N individuals we have d_n positions paired with $d_n * q_n$ random positions (depends on the perceptual range of animal n). The aim was to estimate the effects of covariates on the selection. The mixed multinomial logit model is appropriate to account for correlation within the data produced by a specific individual and also for heterogeneity between different individuals. We estimated the parameters of a mixed conditional logistic regression model using the package TwoStepClogit version 1.2.1 (Craiu et al., 2012).

We used roe deer and red deer data for model parameterization. We only used relocations from summer (June, July, August) to reduce possible confounding disturbances of seasonal effects. Information about the data of roe deer can be found in the methods section of Paper I and II. Information about the data of red deer can be found in the methods section of Paper III. For the analysis, we used no more than one location per hour to homogenize the fix location sampling regime among individuals.

Simulation

Each individual was initialized with identity, sex, its home range centre and a perceptual range.

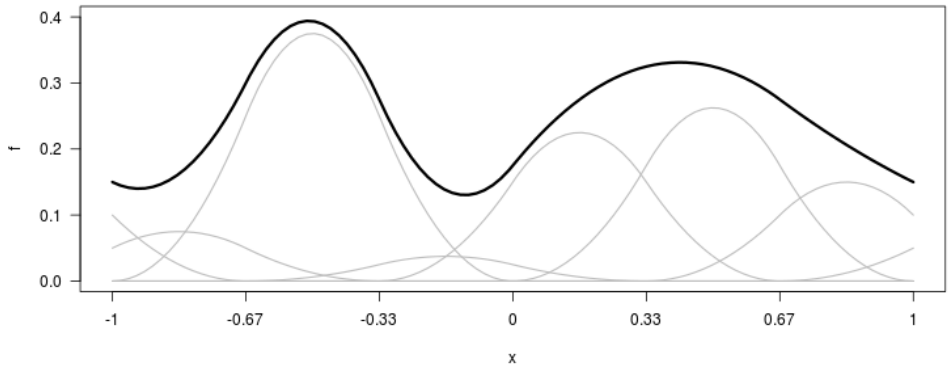


Figure IV.2: The concept of a cyclic B-spline. A cyclic smooth curve (black line) between the interval [-1,1] is built up of 6 B-spline basis functions (grey lines). The B-spline basis functions are non-zero over only 3 intervals, whereby 3 basis functions overlap within one interval. Basis functions multiplied by their associated coefficients (as shown) and summed up yields the spline itself, represented by the black line.

Cyclic B-splines

B-spline curves present a convenient way of modelling time-varying variation of the influence of covariates on site selection. B-splines are defined as piecewise polynomials which results in a high flexibility (Wood, 2006). Basis functions of a B-spline basis are strictly local meaning that multiple parameters build a curve whereas each parameter affects the curve only within the intervals where the corresponding basis function is non-zero (Fig. IV.2). The number of basis functions (rank) indicates the flexibility of the curve, the greater the more flexible. However, the greater the rank the higher the degrees of freedom in our model. We therefore wanted to find the optimal number of basis function that is needed to model time-varying behaviour.

Applications

Patterns of movement trajectories (summary statistics)

We tested for the predictive ability of the model by comparing simulated with empirical movement trajectories (Fig. IV.3). In the attachment there is an animation showing first the path as it was observed from a adult male roe deer (Nikolaus_observed.avi)

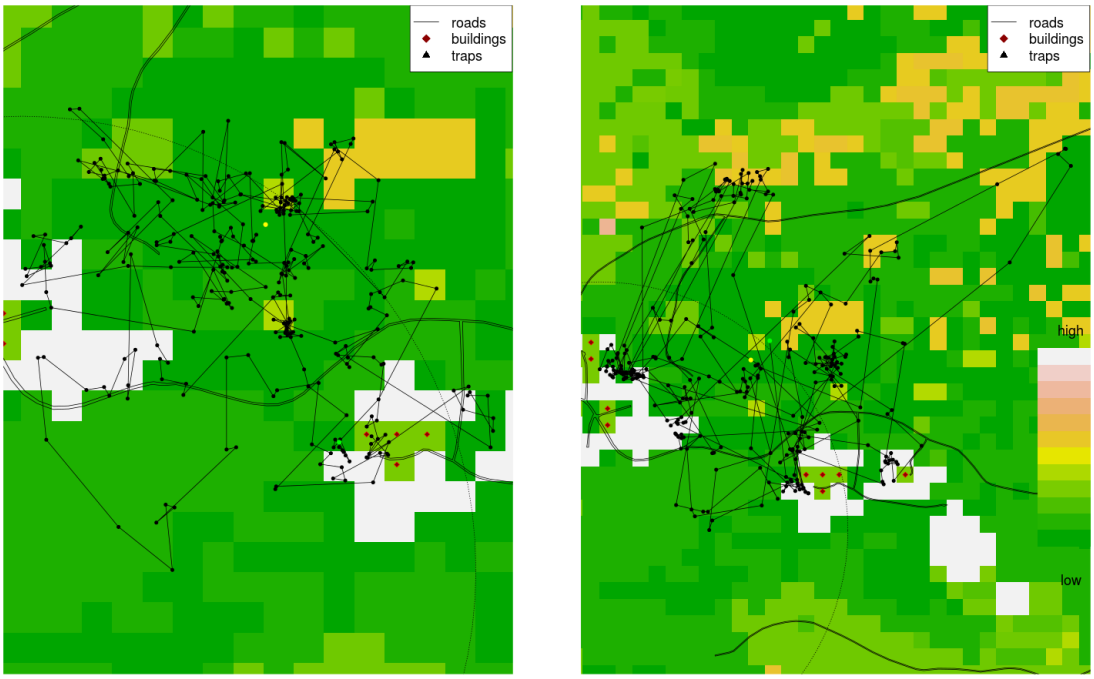


Figure IV.3: The comparison of simulated (left) and observed (right) paths can be achieved with respect to various summary statistics. In our analysis we have included home range size, distribution of step length, variation of attraction to and repulsion from environmental factors like buildings, roads, home range centre, food and cover availability. The observed path comes from a female adult roe deer.

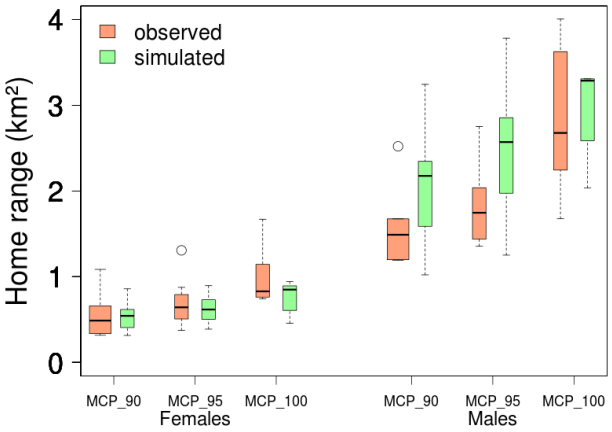


Figure IV.4: Comparison of simulated and observed paths with respect to home range size. The area of the home range is calculated as the area of smallest possible convex polygon that encloses all positions of an animal, called maximimum convex polygon (MCP) method. MCP_90 and MCP_95 refers to a MCP where 90 and 95 percent, respectively of the relocations are used. The 5 and 10 percent, respectively, of the relocations that are removed are outliers with respect to the distance to the home range centre. Females have in general smaller home ranges than males. Home range sizes of simulated paths and observed paths are about the same size.

and second when it was simulated based on the model parameterized with the observed data (Nikolaus_simulated.avi). Different summary statistics have been applied in the past. By far the most commonly used summary statistics is the frequency distribution of step length (Fig. IV.5) and the home range size (Fig. IV.4) as it is fundamental to the movement process (Moorcroft et al., 2006; Dalziel et al., 2008; Rupp and Rupp, 2010; Gautestad et al., 2013). We further aimed to test whether diurnal variation of attraction to and repulsion from environmental factors like buildings, roads, home range centre, food and cover availability are analogous for empirical and simulated data (Fig. IV.6). Of course, we tested only for patterns that are mimicked in our model.

Individuality in temporal variations of movement behaviour

The temporal variation of the effect of each covariate on the movement behaviour were estimated by using B-splines (Fig. IV.2). We found that the effect of most covariates (e.g. step length, cover, food, distance to builings, etc.) varied over the time of day (Fig. IV.2). Less pronounced are variation over time of day for distance to roads and home

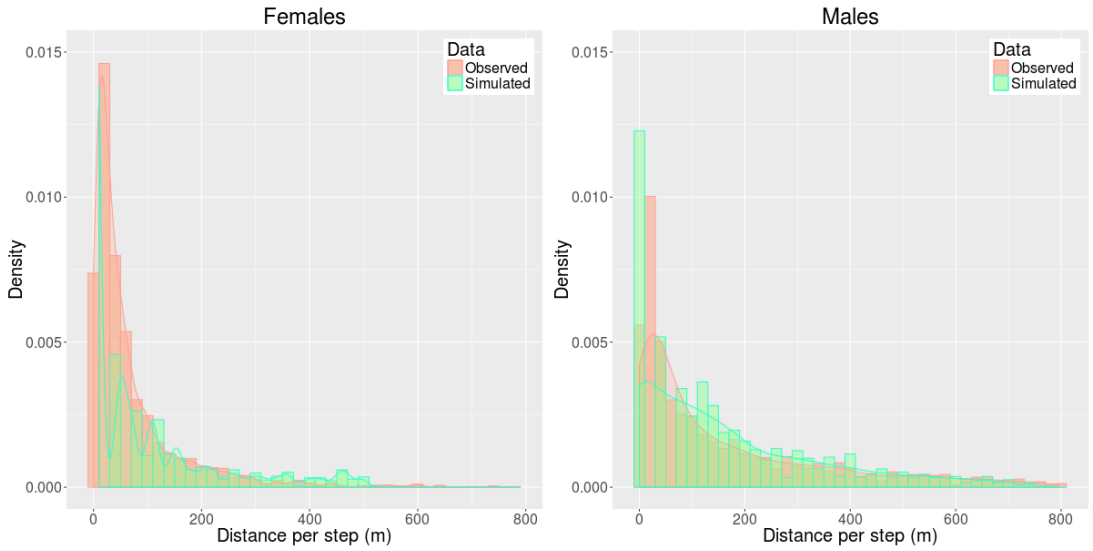


Figure IV.5: Comparison of simulated and observed paths with respect to the distribution of step lengths between relocations.

range centre for female roe deer (not shown). However, for red deer we found significant variations of the effect of all covariates (Fig. IV.7). We also calculated and visualized the deviation of each individual from the population mean (red lines in Fig. IV.7). By visual inspection, we found that for some covariates the variation in movement behaviour was surprisingly synchronized, such as for distance to roads, step length and attraction to food. In contrast, a high degree of individual deviation was found for distance to buildings and home range centre and for attraction to cover.

Use of the model

Our model combines a model for the probability of presence with movement metrics. Probability of presence is independent from the temporal resolution which is appealing as the temporal resolution is a great issue in modelling animal movement (Yackulic et al., 2011; Nathan et al., 2008). Patterns of simulated paths resemble quite well those observed in nature (Fig. IV.4, IV.5, IV.6). Thus, the forward simulation provides realistic pathways with respect to the patterns under study.

However, we applied the patteren-oriented approach by simple visual inspection. This approach was originally established as support in the model parameterization process (Grimm et al., 2005). However, inverse modelling required a high computational effort when many parameters have to be estimated as this involves a respectively higher num-

ber of corresponding patterns (Wiegand et al., 2003). A forward modelling approach, where parameter are estimated in a first step, as we have shown in our study, may be advantagous in terms of computational time.

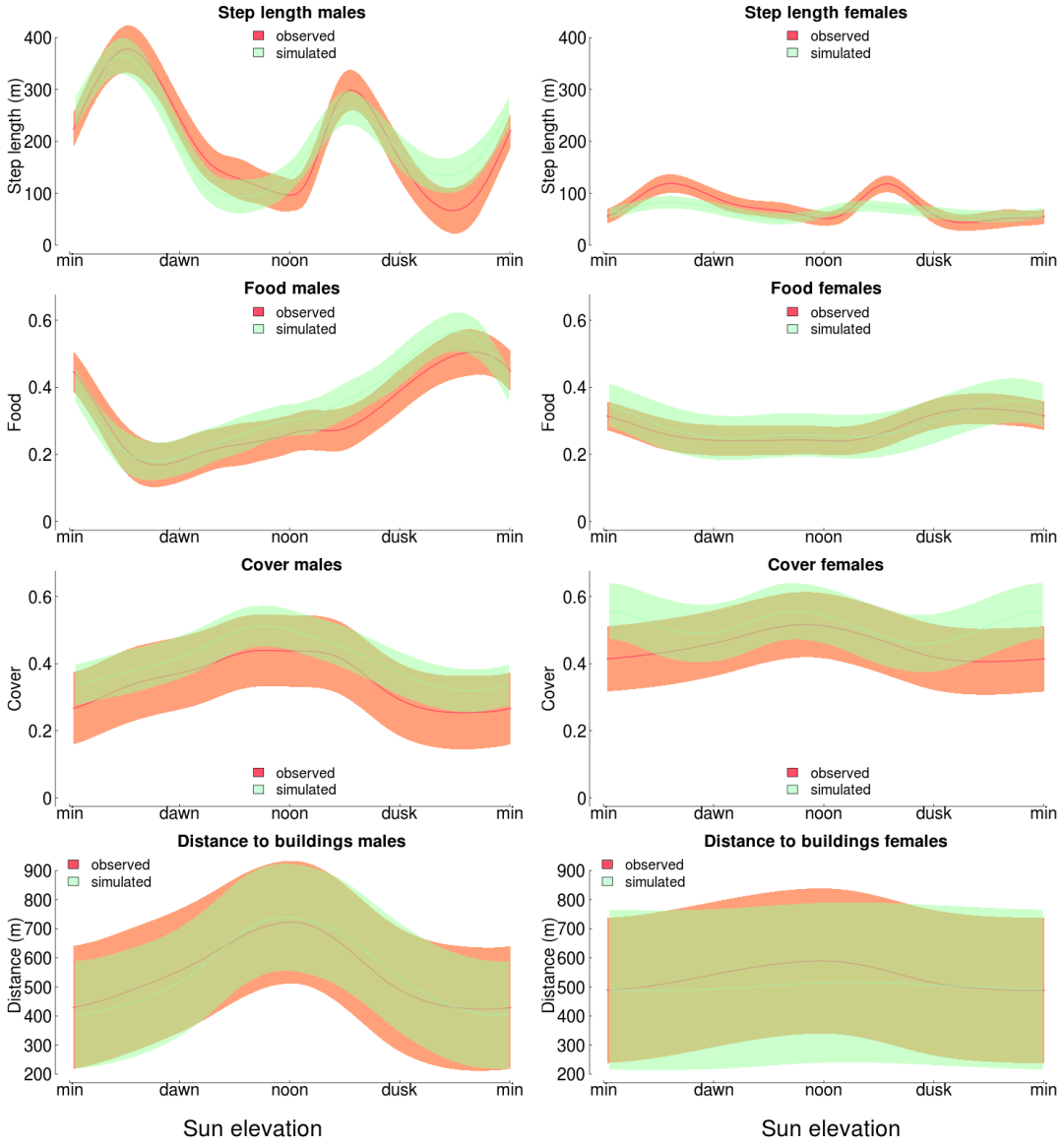


Figure IV.6: Comparison of simulated and observed paths with respect to diurnal variations in step length, the selection of food and cover and avoidance of buildings on the population level differentiated between males (left) and females (right). GPS-based locations of observed paths originates from 11 females and 9 male roe deer recorded in June 2006/2007 in the Bavarian Forest National Park.

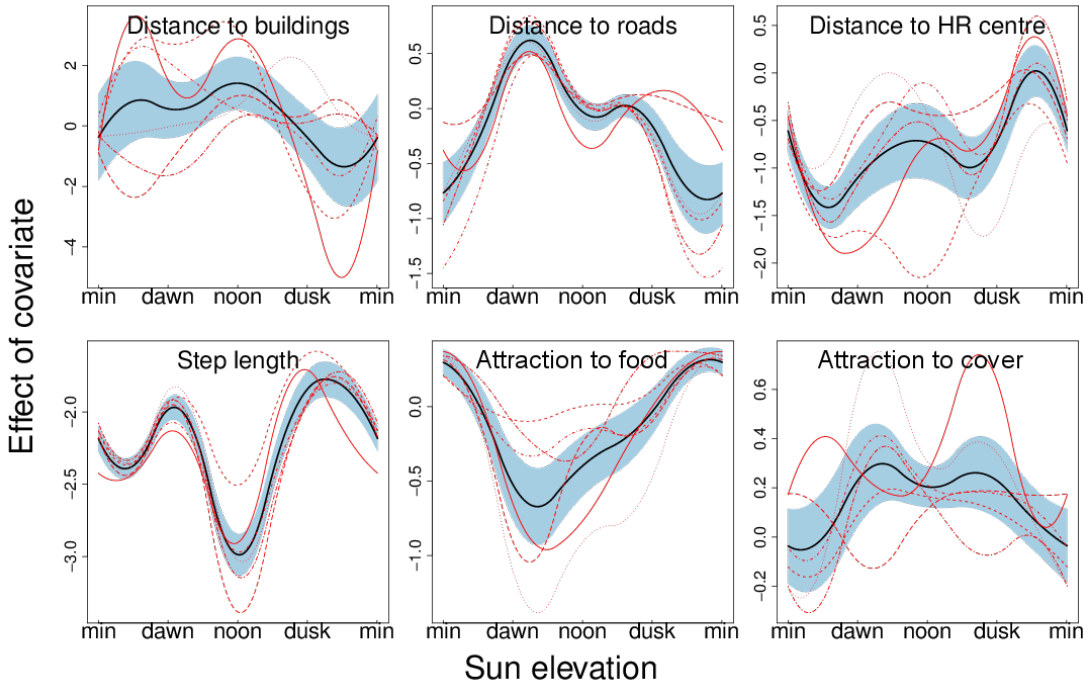


Figure IV.7: Variation of the effect of covariates over the time of day (sun elevation) for female red deer in June 2006/2007 calculated with cyclic B-splines. Black line indicates the population mean with standard error in blue shade. Red lines show the estimates for the 6 individuals. Individual deviation is calculated with random effects for each coefficient building up the splines (Fig. IV.2).

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2nd author

List of second author research paper

Paper V

M. Ewald, C. Dupke, M. Heurich, J. Müller, and B. Reineking

LiDAR remote sensing of forest structure and GPS telemetry data provide insights on winter habitat selection of European roe deer

– Forests, 5(6):1374–1390, 2014.

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Paper VI

E. Ludes-Wehrmeister, C. Dupke, T. C. Harder, W. Baumgärtner, L. Haas, J. Teilmann, R. Dietz, L. F. Jensen, and U. Siebert.

Phocine distemper virus (pdv) seroprevalence as predictor for future outbreaks in harbour seals

– Veterinary Microbiology 183:43–49, 2016.

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Paper VII

Ulrike Märkel, Claudia Dupke, Benno Wölfing, Marco Heurich

Activity patterns of roe deer and the time of day are more important than habitat selection in determining predation risk by Eurasian lynx

in preparation

Chapter 3

Synthesis and outlook

3.1 Synthesis

Patterns of animal distribution on large scale are associated to the dynamical interaction between the internal state of individual animals and the environment on small scale. Relocation data of animals can be regarded as a reflection of this process. The aim of this thesis was to provide an overview of how relocation data of moving animals can be analysed with respect to habitat selection. In the introduction, methodological obstacles in the field of the analysis of GPS-based location data were identified. The aim was to sensitize researchers to adapt research-related decisions to the actual research question. An overview of possible approaches towards habitat selection was given in which relocation data of various temporal resolutions are related to spatial data that describe the environmental conditions in the surrounding of an animal. Statistical methods were presented that enable the researcher to describe the conditions which make a site attractive or unattractive to an animal. Characteristics of the population and/or the environmental conditions are usually averaged together.

In research paper 1 and 2 we quantified habitat selection of roe deer in the Bavarian Forest National Park. GPS-based locations of roe deer were analysed with respect to habitat selection.

In research paper 1 we show that temporal variation and the predictability of limiting factor is essential to understand spatial patterns of animal movement on small but also on larger scale. We argue that temporal scales have received insufficient attention in past studies in contrast to the role of spatial scale in the study of habitat selection. Even though it is well known that spatial and temporal scales often co-vary in most ecological processes. Some studies have shown that the use of certain habitats by animals differ for different times on different temporal scales (e.g. winter vs. summer or day vs. night). However, based on our high temporally resoluted GPS position data we show that seasonal and daily temporal scales interact with each other. We

further link the temporally varying patterns of habitat selection with resource use, namely food and cover. Earlier studies have shown that prey species such as large herbivores trade off between foraging and protection. We confirm this trade-off with respect to protection from human disturbances and further show that this trade-off is also subjected to temporal variations. However, we found no hints that roe deer aim to reduce predation risk by lynx through habitat selection behaviour. We conclude that habitat selection patterns by large herbivores varied across temporal scales in terms of ecological drivers, variation and predictability. The following three generalisations are derived: i) Habitat selection at the different scales may be the consequences of the temporal variation and predictability of the limiting factors as much as its association with fitness. ii) The landscape of fear might have less importance at the studied scale of habitat selection than generally accepted because of the predator hunting strategy. iii) The difference in habitat selection at the 2nd and 3rd order is supposed to be greater for wider ranging herbivores.

Given the continuous process of movement over time by roe deer that we clearly show in research paper 1, we are convinced that studies would benefit from using smoothing spline functions (in generalized additive mixed effects models) when analysing temporal variation of habitat selection. A continuous consideration of habitat selection has rarely been shown in literature. In contrast, the alternative of a categorization of a continuous variable, as usually done in other studies, always involves a loss of information, namely the data of other time slots. An analysis based on smoothing splines uses all data at the same time.

In research paper 2 we illustrate that incorporating functional response in habitat selection studies is biologically meaningful and technically essential. Most statistical models used to analyse habitat selection data like RSFs or SSFs assume a proportional selection of a given habitat according to its relative availability (Aarts et al., 2013). This assumption has been criticized as it limits or restricts the generality of a study (Moreau et al., 2012). We relaxed this assumption by entering relative availability as an offset variable assuming a proportional selection with availability (coefficient forced to 1) and by adding an additional non-linear effect of relative availability. This parametrisation of the model is particularly useful for describing the so-called functional response of habitat selection (Mysterud and Ims, 1998). Functional response was originally described for a changing consumption rate of a predator with respect to the density of its prey (Holling, 1959). Later it was transferred to habitat selection, where it was defined as the change in relative use of habitats with changing availability (Mysterud and Ims, 1998).

Indeed, in our analysis of roe deer functional response was evident for almost all habitats. We have shown that selection for habitats differs between seasons and times of day and so do the curves for functional response. Different shapes of the curve for functional response for different times of day and seasons support the finding that

primarily the needs of the animals and to a much lesser extent the availability of a habitat determines the use of a habitat. Habitat are not selected per se but are selected for what they provide to animals. Roe deer has to choose between habitats offering partially opposing resources. For example, meadows provide good quality forage but no shelter and contrary, old forest stands provide shelter but only low quality forage. The selection of habitats by herbivores is characterised by balancing between the need for food and cover (Godvik et al., 2009). We show that this trade-off results in a adaption of selection with respect to the internal needs that can be satisfied in a habitat and to a lesser extent to its availability. Hence, functional response is the consequence of this trade-off (Mysterud and Ims, 1998).

To our knowledge, this is the first study after the seminal paper of Mysterud and Ims (1998) that truly related relative use of habitat to availability. In consequence of this, we were the first who linked patterns of functional response in habitat selection to Holling's types I, II, III and IV (Holling, 1959). This was possible as we used baseline-category logit models that account for the multinomial choice of roe deer when selecting a habitat. Usually, when studies aim to detect functional response they showed varying selection strength or selection coefficients with increasing availability of a habitat. We therefore provided conceptual plots that shows a link between variation of selection strength of a habitat with increasing availability and the variation of use of a habitat with increasing availability. However, we indicated that the shape of the curve that relates selection strength with availability is not necessarily a pointer to the shape of the curve that relates use and availability. Consequently, with RSF it is hardly possible to detect the Holling type correctly.

In research paper 1 and 2 we focused on temporal and spatial variation in habitat selection. It is obvious, that considering time (of day and year) and the availability of habitat is crucial to understand habitat selection of herbivores. In our analysis, both sources are included in a discrete choice model to explain the variation in the selection of a specific habitat. Furthermore, we also accounted for variation among individuals by integrating a random factor for the individuals in the model. However, we did not *quantify* individuality as a source of variation in habitat selection in these studies. Instead, we provided a quantification of the degree of individuality in research paper 3. For this, we used a step selection function (SSF, paragraph 1.4.5.2) approach that estimates habitat selection with respect to a covariate (*i.e.* cover) at the population level while accounting for variations among and within individuals. We proposed a framework that obtains unbiased estimates for the population-level habitat selection strength, for the variation among individuals, and the within-individual variance. The latter two quantities are then used to calculate the value of repeatability of the habitat selection behaviour (Nakagawa and Schielzeth, 2010). The framework was validated on simulated data and tested on GPS-based location of red deer recorded in the Bavarian

Forest National Park in 2006/2007. As expected, we found diurnal variation in habitat selection with respect to cover on the population level. Moreover, results suggested that variation among individuals differ for different times of day. For example females, exhibited a high degree of individual behaviour during day, as differences among individuals were greater and variances within individuals were relatively low during daytime compared to other daytimes. This means that during daytime female individuals are consistant and, hence, more predictable in their habitat selection behaviour on the individual-level, however, the variety of behaviour between individuals is greater and makes it less predictable on the population level.

Inferences on the response of animals to various environmental factors helps to understand the ecology of animals and to make predictions. However, inferences and predictions based on descriptive statistical models (*e.g.* RSF, discrete choice models, SSF) should be referred to the specific study area and are difficult to be generalized to other areas. This is because the response of an animal to environmental factors may depend also on other factors that are either constant in the study area or not included in the analysis and may be different in other areas such as predation risk, density of conspecifics, forage quality or disturbances, to name a few. Hence, the predictive ability of descriptive statistical models is limited due to the rather static nature of this modelling approach.

However, considering movement as the behavioral mechanism that precedes habitat selection, leads to dynamic models that integrate the movement process in the analysis. IBMs (section 1.5) offer a model technique that is able to capture the movement process on a small scale and to reconstruct realistic ecological patterns on broader scales. Hence, IBMs can help to understand broad scale phenomena by simulating a series of single movement decisions of multiple individuals. We presented such a model in research paper 4 that is able to produce realistic simulated paths with respect to home ranges sizes, step length distribution, temporal variation in the selection of resources (*i.e.* food and cover), temporal variation in avoidance of disturbances such as settlements and roads, temporal variations in step lengths and exploiting behaviour.

3.2 Outlook

This work focused rather on the methodology in habitat selection studies. In particular in research papers 3 and 4 we did not provide any ecological theories or implications. However, all applied frameworks are dedicated to serve in planning wildlife management and conservation. Approaches presented in this theses are designed for gaining knowledge about the ecology of species which is essential before planning conservation strategies. In particular, as explained in detail in the introduction, movement of animals is a core component in sustaining biodiversity in ecological systems and needs therefore

to be incorporated in conservation management (Jeltsch et al., 2013). The urge has been identified and first publications provide suggestions for how wildlife management can benefit from movement ecology (Allen and Singh, 2016).

First, habitat selection studies can help to describe the conditions that make a habitat suitable for a species (Bjørneraas et al., 2012). In particular, factors can be identified that influence the fitness of animals. For this, proxys of fitness that measure the population's performance such as survival or reproduction rate can be related to habitat selection (McLoughlin et al., 2005, 2006). Models that relate habitat conditions to habitat selection can be used to make predictions about the distribution and abundance of a species (under certain conditions, though, Guisan and Zimmermann, 2000; Boyce et al., 2016). For example, Moreau et al. (2012) analysed habitat selection for the threatened woodland caribou (*Rangifer tarandus*) and found that the selection of old growth forests increased with increasing effects of forestry (clearcut areas) in the direct surrounding. The conservation relevance is obvious, however, this application also illustrates the importance of biologically meaningful models through *e.g.* integrating concepts such as functional response in the analysis. We covered this in research paper 2.

Second, the question of scale was discussed several times in this thesis (e.g. research paper 1). Certainly, it is important in modelling habitat selection, but also in planning management actions. Finding the right scale of management that is effective requires an understand of "where, when, how and why animals move" (Allen and Singh, 2016). Klar et al. (2008) implemented fine-scale habitat selection models for the European wildcat (*Felis silvestris*) with which potential reintroduction sites were identified. They suggested to enlarge and connect those small areas of suitable habitats. This may involve localized management actions but the greater network of areas that would arise would be of greater scale. Hence, even though conservation is needed on a large scale, management actions may be required on a small scale for specific problems. This can be identified when movement and habitat selection behaviour of the focal species is known. Also, knowledge about temporal variation in movement behaviour can be an important guide in conservation. For example, the route of Southern bluefin tuna (*Thunnus maccoyii*) during annual winter migration intersects with a year-round tropical tuna longline fishery. Hobday and Hartmann (2006) suggested to exclude fishery in those areas where the Southern bluefin tuna, a quota-managed species, is predicted by a real-time habitat model that bases its prediction on *e.g.* temperature preference.

Third, due to the ongoing process of climate change, animals are faced with a rapid alteration and loss of environmental conditions their behaviour, in particular movement behaviour, is adapted to. The question arises whether and to what extent animals are able to adjust their behaviour to changing quality and distribution of habitats. The degree of plasticity in movement behaviour refers to the ability of animals to adapt movement to environmental changes such as deterioration of local conditions or habi-

tat loss on broader scale (Cagnacci et al., 2011). The degree of phenotypic flexibility of animals towards changing conditions is likely linked to the fitness of its population (McNamara et al., 2011). Hence, the detection of factors that influence the plasticity of a species' behaviour is of direct value for conservation planning (Winkler et al., 2014). With our study about quantifying repeatability in habitat selection behaviour of animals (research paper 3) we provide a framework that can quantify the degree of plasticity in animal movement behaviour towards an environmental factor. Identifying environmental stressors that affect trait variation and repeatability is crucial in evaluating possible management strategies which has been reviewed for fishes (Killen et al., 2016). Also, for whooping cranes (*Grus americana*) Teitelbaum et al. (2016) showed that experienced individuals exhibited a higher plasticity in movement behaviour in response to environmental change than younger individuals. Hence, for example managment strategies such as selective harvesting to manipulate age- or sex-structures in populations require theoretical investigations in advance to avoid undesired evolutionary and behavioural consequences (Milner et al., 2007).

Fourth, the type of movement in populations, such as being sedentary or exhibiting migration, dispersal or nomadism, is essential for management actions (Allen and Singh, 2016). The type of movement has direct implications for the necessity of maintaining connectivity with *e.g.* corridors (Kramer-Schadt et al., 2004). In addition, characteristics of movement such as "movement pathways, distance and timing of movements, shapes and sizes of home ranges, habitat selection along movement paths [need to be understood for] planning, designing and implementing management actions" (Allen and Singh, 2016). This exactly is, what the IBM presented in this thesis was meant for; understanding the movement process of animals (research paper 4). Furthermore, if an IBM accounts for plasticity in the movement behaviour of animals, it can be applied to make predictions of animal movements in a changing environment (Latombe et al., 2014). This is particularly necessary, when management scenarios need to be evaluated in advance. For example, Kanagaraj et al. (2013) used an individual-based, spatially explicit dispersal model to quantify inter-patch connectivity between habitat patches for tiger (*Panthera tigris*) in India and Nepal. Simulations of corridor restoration scenarios strengthened their assumption that current conditions leading to declining tiger populations, may be mitigated by the implementation of tested management actions.

Finally, predictions based on a model can only be as good as the model is. LaPoint et al. (2013) predicted corridors of fishers (*Martes pennanti*) based on GPS-based data and a weighted compositional analysis (see section 1.4.2) for fisher habitat selection. However, when predictions were compared with data from camera traps, strong divergence were assessed. The authors discussed multiple reasons that may have lead to the little overlap. All were, of course, linked to decisions made during the model process. Consequently, in the last sentences of this thesis I would like to put emphasis on a responsible awareness of the researcher modelling habitat selection of animals. It is

important to bear in mind that a model is a very simplified version of reality, hence, we will not make out the truth. A mathematical model is only a tool to gain knowledge about the underlying ecological process. Whenever we implement models for making predictions, we have to have in mind all our assumptions we made during the model process. Hence, predictions are always built on a suite of assumptions that are sometimes controverse, arbitrary, or even unwitting. Predictions are also associated with uncertainties which have to be reported and discussed. Nice-looking patterns must not tempt researchers to hide great uncertainties - I know that there is such a temptation. Furthermore, we are able to set up highly complex models that we can combine with huge real data sets, thanks to the availability of low-cost computing power. However, just because so much is technically and creatively possible, does not necessarily mean it helps to answer the questions of our research. The challenge is to select the appropriate level of complexity that the model can still be understood in terms of the effect of input on output and most notably capture the process the researcher aims to understand. As long as we aim to do natural science we are under the obligation to serve nature and we can do this best, if we we are aware of and communicate our strengths and weaknesses in modelling.

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Electronic Appendix

No.	File/Folder	Description
A	correlated_random_walk.gif	Simulation of a correlated random walk in a simulated landscape
B	Animation_Appendix6.mpg	Animation shows selection probability for all habitat types over time of day running over time of year
C	Nikolaus_observed.avi	Animation of the locations a male roe deer visited between January 2008 and April 2009 in the landscape of the Bavarian Forest, whereby the map shows the availability of food assessed in June.
D	Nikolaus_simulated.avi	Animation of the simulated locations based on the locations of a male roe deer (see above) in the landscape of the Bavarian Forest, whereby the map shows the availability of food assessed in June.
E	FunResp (folder)	R package for the analysis of habitat selection of animals with multicategory logit models (including manuals)
F	run_analysis.R	R-Code that applies package FunResp to analyse movement data
G	IBM (folder)	Contains all data and R-code to analyse and to simulate movement data using an IBM

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S.D.G.

(Eidesstattliche) Versicherungen und Erklärungen

(§5 Nr. 4 PromO)

Hiermit erkläre ich, dass keine Tatsachen vorliegen, die mich nach den gesetzlichen Bestimmungen über die Führung akademischer Grade zur Führung eines Doktorgrades unwürdig erscheinen lassen.

(§8 S. 2 Nr. 5 PromO)

Hiermit gebe ich mein Einverständnis, dass die elektronische Fassung meiner Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung hinsichtlich der eigenständigen Anfertigung der Dissertation unterzogen werden kann.

(§8 S. 2 Nr. 7 PromO)

Hiermit erkläre ich eidesstattlich, dass ich die Dissertation selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe.

(§8 S. 2 Nr. 8 PromO)

Ich habe die Dissertation nicht bereits zur Erlangung eines akademischen Grades anderweitig eingereicht und habe auch nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden.

(§8 S. 2 Nr. 9 PromO)

Hiermit erkläre ich, dass ich keine Hilfe von gewerbliche Promotionsberatern bzw. -vermittlern in Anspruch genommen habe und auch künftig nicht nehmen werde.

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